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Vol. 74 MAY-JUNE, 1947 No. 3

Bulletin
of the
Torrey Botanical Club
and
Torreya

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Published for the Club bi-monthly
by
THE SCIENCE PRESS PRINTING COMPANY
N. QUEEN ST. AND McGOVERN AVE.
LANCASTER, PENNSYLVANIA

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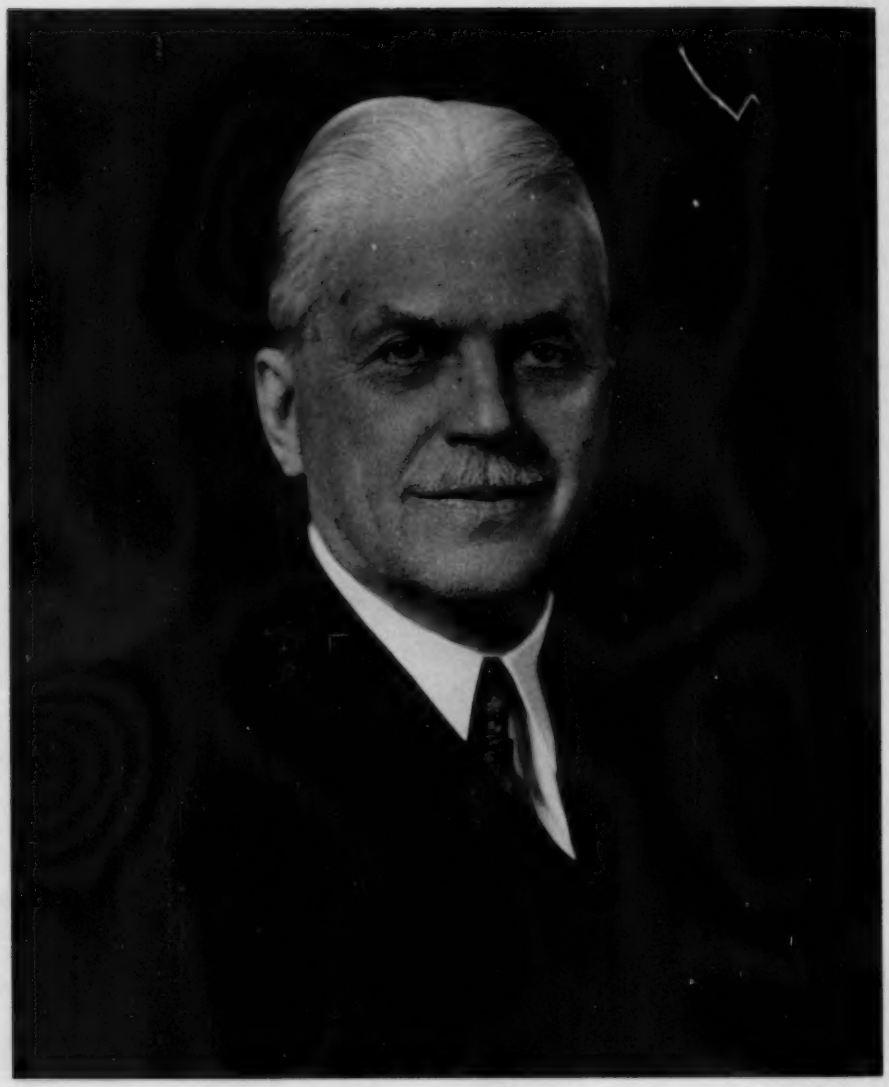
Claims for missing numbers must be made within 60 days from the date of issue.

The subscription price of the Bulletin of the Torrey Botanical Club (including Torreya) is $7.00 a year except to active members of the Club. Of the annual membership dues, $3.50 covers a year's subscription to the Bulletin.

Entered as second-class matter October 8, 1940 at the post office at Lancaster, Pa., under the Act of March 3, 1879. Accepted for mailing at the special rate of postage provided for in the Act of February 28, 1925, embodied in paragraph 4, section 538, P. L. & R.



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BERNARD OGILVIE DODGE

UNIV. OF MICH.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 3, PP. 197–198 MAY, 1947

BERNARD OGILVIE DODGE

FRED J. SEAVER

Of all the living ex-presidents of The Torrey Botanical Club probably none has been more active in the affairs of the organization than Dr. B. O. Dodge who, with the loyal cooperation of his good wife, has held about every position which the Club afforded.

He was Secretary-Treasurer at the time when that title covered a multitude of duties, such as recording the minutes; collecting money and keeping records of all receipts and expenditures; negotiating contracts with the printers; writing letters; and, last but not least, delving into the depths of the subcellar at Columbia University, ferreting out from the dust-covered stock and debris back numbers of the Bulletin, and shipping them to every part of the world. In that day the Secretary-Treasurer was "Jack of all jobs" in connection with the Club. For several years he was editor of the BULLETIN and for many years he collaborated with Mrs. Dodge who was the official Bibliographer. In fact there is scarcely an activity of the Club in which the Dodges have not been concerned. For these reasons it has been thought appropriate to dedicate the present volume to Bernard Ogilvie Dodge.

The writer's first encounter with Dr. Dodge was in the fall of 1909 when the latter entered Columbia University as a graduate student, and reported to the New York Botanical Garden for research in the fungi; in this group he had acquired an interest while engaged in high school work in Wisconsin, and he maintained this interest later in the University of Wisconsin. He was assigned to work on the Ascobolaceae, a family of the Discomycetes, with the expectation that he would carry on a taxonomic study of the family. He soon became interested in the reproductive processes of these fungi; this was the beginning of his work on sex in the fungi, in which field he has made his chief contribution to science. One of his early papers was "Methods of culture and the morphology of the archicarp in certain species of Ascobolaceae" (Bull. Torrey Club **39**: 139–197. *pl. 10–15.* 1912). In this group he described a new species, *Ascobolus magnificus.* It was in connection with this work that he discovered the effect of heat in inducing germination of the ascospores of *Ascobolus,* a process which was later found applicable to the germination of the spores of other fungi, especially *Neurospora.* He continued his researches in Columbia University until 1920, working also with the plant rusts which took him into the field of pathology.

In 1920 he went to Washington as Plant Pathologist in the United States

Department of Agriculture where, although a Plant Pathologist by vocation, he continued his investigation on sex in the fungi and extended it to other groups. In his well known work on pink bread mold (*Neurospora*) he was a pioneer in the hybridizing of fungi and systematically observing the results of such crosses. Through this work he became one of the world's most outstanding mycogeneticists. His work on *Neurospora* is too well known to require here more than a passing mention.

In 1928 he accepted the position of Plant Pathologist at The New York Botanical Garden and began his work on May 1 of that year; he officially retired at the end of 1946. During his official connection with the Garden he has contributed much toward the improvement of the health of the plants of that institution, especially in the control of black spot of roses. He discovered the cause and control of a disease of the much cultivated *Pachysandra*. The disease is caused by the fungus *Pseudonectria pachysandricola*, a species described by Dr. Dodge and not previously known to science.

A scientist never really retires, he merely throws off some of his routine duties in order to devote himself more exclusively to his hobby; and Dr. Dodge is no exception to the rule. He may still be seen daily in his laboratory and will doubtless continue his researches with unabated zeal.

His book *Diseases and pests of ornamental plants*, prepared in collaboration with Dr. H. W. Rickett, is in constant use by pathologists and is the only work of its kind devoted exclusively to diseases of ornamental plants.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 3, PP. 199–214 MAY, 1947

GROWTH CURVES OF ORIENTAL TOBACCO AND THEIR SIGNIFICANCE[1]

FREDERICK A. WOLF

From time immemorial biologists have been concerned with problems of growth. Consequently a voluminous literature on growth, including observations on both animals and plants, has accumulated. In attempting to interpret this literature and to seek an understanding of the underlying principles involved, many controversial issues have been brought to light. Judging from perusal of representative botanical investigations it would appear that all too little which is basic is yet well established. This conclusion confirms that of Glaser (1938) who stated that "When reduced to absolute dryness, a fair sample of the literature on organic growth yields a residue in which a few non-volatile platitudes are embedded in a voluminous matrix of quantitative fact."

In his recent book, "Growth and Form," Thompson (1945) evaluates the present status of knowledge of growth as it relates both to animals and to plants. It appears that present-day concepts regarding growth in plants, including both woody and herbaceous species, date from the work of Sachs (1887). His observations show that the growth of broad bean, *Vicia faba* L., begins at a slow rate but as the process continues it does so at an increasingly rapid rate until it reaches a maximum; then growth progressively decreases and eventually comes to a stop. This sequence of events may be portrayed graphically by an "S-shaped" or sigmoidal curve, now generally recognized as a common pattern among Nature's mechanisms ("mecanisme commun aux phenomenes dispartes"). Furthermore Sachs' measurements of the growth rate of the shoot-axis of *Phaseolus multiflorus* Willd. and of dahlia, if graphed, yield curves similar to that of broad bean.

Among other annual species in which growth rates have been studied are *Vallisneria spiralis* L., by Bennett (1880), maize, by Stefanowska (1904), Lehenbauer (1914), and Pearl and Surface (1915), and sunflower, by Reed and Holland (1919). It has been concluded that the precise form of the logistic or growth curve for each of these species, or, indeed, for any other species or particular individual is determined by two basic variables, one germinal and the other environmental, which interact during the develop-

[1] This investigation of oriental tobacco and others previously reported were financed, in part, by the General Education Board. Acknowledgment is made of help by Dr. P. M. Gross, who critically read the manuscript, and by Walter S. Clark, who collected some of the data.

mental period. As is generally appreciated, the former is constituted of a complex of internal factors and the latter of interdependent external factors.

The writer has been concerned for several years with problems of growth in connection with the production of oriental types of tobacco (Wolf & Jones 1944, Bentley & Wolf 1945, Wolf 1946). From experience gained during the course of this work, it has become increasingly apparent that a better understanding than is extant is required regarding growth of the tobacco plant, if improvement in quality and quantity of the product grown is to be secured. On the basis of published results with tobacco (Avery 1934, Morgan & Street 1935, Petrie, Watson & Ward 1939, Petrie & Arthur 1943), and with other plant species, one might logically assume that there is little likelihod of achieving this purpose or that little additional knowledge would be acquired by studying the rate of growth of tobacco. Nevertheless additional observations on growth of this crop plant have been made and the data thus secured together with their interpretation are presented herewith.

MATERIALS AND METHODS

The varieties of oriental types of tobacco used in these studies included Izmir (Smyrna), Broussa and Dere (Samsoun), Stanimaka (Cavalla), and Yaka (Xanthi). They were grown in a field at the Tobacco Experiment Station, Oxford, N. C. The cultural practices employed, including fertilization, spacing of plants, and tillage, were such as are known to be favorable for satisfactory growth. Two methods of sampling were employed. In one method, increase in height of selected plants was determined by a series of successive measurements extending over a period of about two months. At the same time the rate of expansion of leaves was followed by measuring the length and greatest width. A ratio between length-width and area had been predetermined, and on this basis leaf area was calculated, using the product of length and width as one factor in the calculation.

In the other method paired groups of ten plants each were selected and marked for analysis. Replications were used so far as time permitted. All plants from one member of the pair were permitted to grow unmolested until the seed heads were well formed. By that time the leaves along the lower portion of the stems had become dry and others above them were senescent. Other leaves, properly primed,[2] from near-by plants therefore were substituted in the analyses for these dry and overmature ones.

The leaves from all plants of the other member of the pair were primed as they matured and their inflorescences were removed as soon as the buds appeared.

In making the analyses, the plants were uprooted and brought into the

[2] Priming is a term used to designate a method of harvesting tobacco by picking the leaves when they are in best condition for curing.

laboratory where the leaves were removed in sequence, weighed immediately, and their lengths and widths were determined. Weights and lengths of internodes were determined after the stems had been cut into segments. The average weight of the leaves at each node and that of corresponding internodes was computed.

RESULTS

The growth form of plants of oriental varieties of tobacco should first be discussed. Their unbranched stems have the general shape of a gradually tapering cylinder, being largest in diameter near the soil level. The internodes tend to become progressively longer from the basal ones upward to the middle of the stalk and gradually shorter thereafter. An occasional plant is found having short internodes occurring between long ones, but from average measurements of corresponding internodes of a series of plants such inequalities are not so apparent. Internode length, moreover, is correlated directly with weight (mass), to such a degree that the internodes of greatest weight are produced at the median stalk region, being progressively less heavy both upward and downward from this median position.

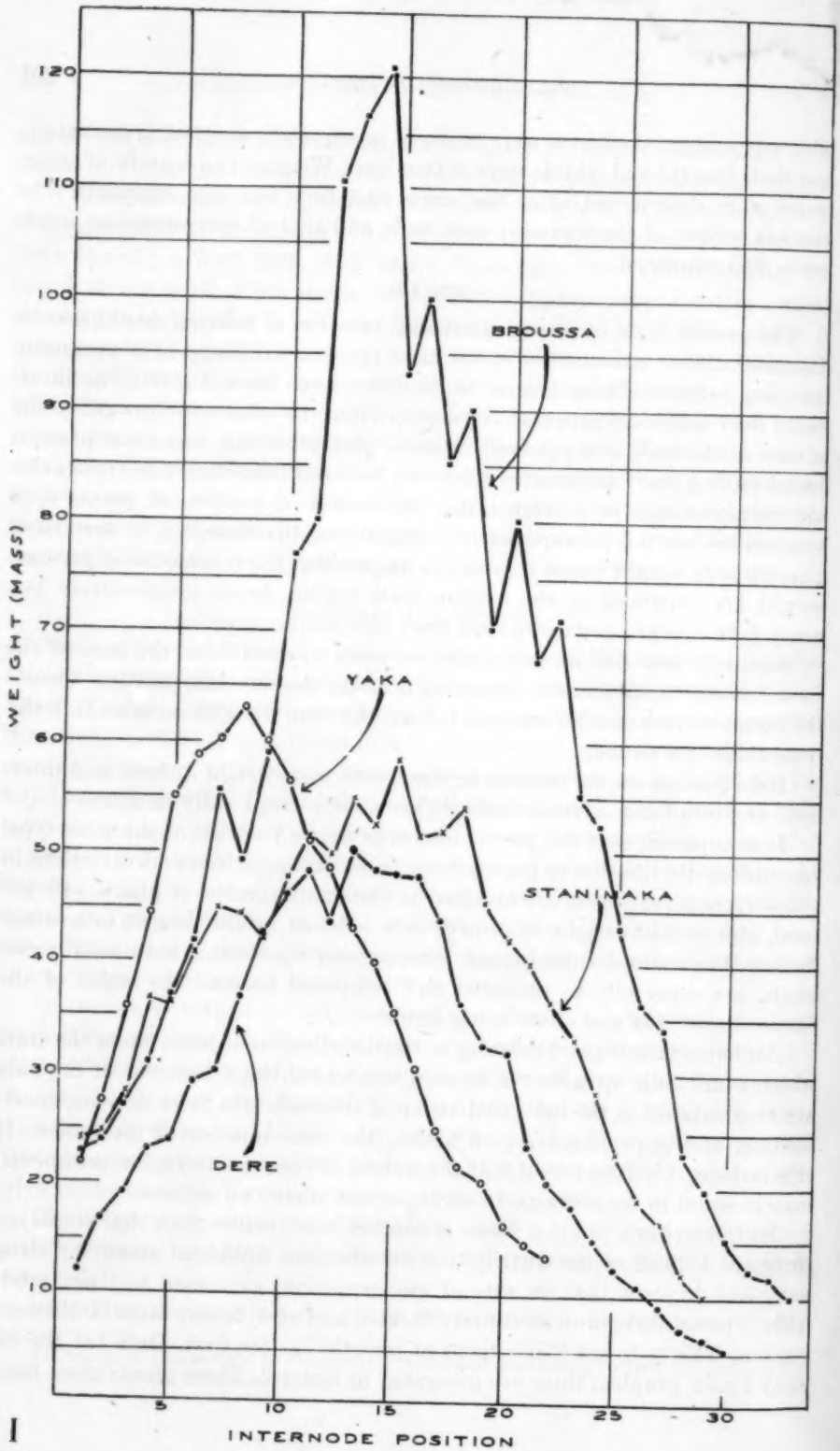
Similarly leaf size progressively increases upward from the base of the stem, those of maximum size occurring near the median stalk position. Thence the leaves become smaller upward toward the stem tip with occasional deviations from this pattern.

Data bearing on the relation between internode weight (mass) and internode position for 4 oriental varieties are shown graphically in figure 1.

It is apparent that the jagged curves in figure 1 are all of the same type, resembling distribution or population curves. Irregularities and variations in shape from ideal curves are ascribed to the small number of plants (10–25) used, and to fluctuations in growth rate induced by differences in weather during the developmental period. Broussa and Stanimaka, both equally tall kinds, are especially to be noted and compared because the stalks of the former are sturdy and of the latter slender.

An important feature relating to the distribution of mass along the stalk which is not fully apparent in figure 1 becomes obvious, however, if the data are recalculated on the basis of division of the stalk into three regions, lower, median, and upper, each region having the same number of internodes. If this is done, it will be found that the weight of the median region is approximately equal to the combined weights of the other two regions.

In the writer's opinion there is another way, better than that employed in figure 1, to show the distribution of substance produced along the stem-axis, and to show that its rate of augmentation, expressed as "per internode," proceeds both in an orderly fashion and at different rates in different regions. This is to use "increment of growth" as the unit. Data for the variety Izmir, graphed thus, are presented in figure 2. These plants grew for a


WEIGHT (MASS)
120
110
100
90
80
70
60
50
40
30
20
10
BROUSSA
YAKA
STANIYAKA
DERE
5
10
15
20
25
30
INTERNODE POSITION

I

period of 86 days after transplantation. The "intervals" herein could with equal propriety be expressed as "per days," so long as it is appreciated that the elapsed time for the development of substance for any internode was not accomplished during an average of about 3 days but rather about 3 weeks. The weights shown are the combined weights of 10 plants, internode weights being combined with that of the corresponding leaf. For each succeeding internode in ascending order the weight of substance produced was added seriatim to that of the previous total. By so doing, the green weight of stem and leaf substance of approximately 20 grams had increased to more than 900 grams by the time the thirty-first segment had matured. Such progressive increases, when graphed, give a typical sigmoidal growth curve (fig. 2) in which change in rate of growth at different intervals is portrayed by change in slope of the curve.

TABLE 1. *Rate of expansion of Izmir tobacco leaves at different stalk positions*

Lower leaves			Median leaves			Upper leaves		
Date	Average leaf area, cm.²	Percentage of mature size	Date	Average leaf area, cm.²	Percentage of mature size	Date	Average leaf area, cm.²	Percentage of mature size
June 7	9.04	8.8	June 27	13.86	12.2	July 18	8.61	18.1
" 10	19.28	18.9	July 1	40.65	35.9	" 23	30.75	64.7
" 13	40.80	40.1	" 4	71.60	63.2	" 25	37.20	78.3
" 17	81.40	80.0	" 8	101.20	89.4	" 29	42.30	89.0
" 20	94.10	92.4	" 11	108.20	95.6	Aug. 1	44.80	94.3
" 24	97.70	95.9	" 15	111.20	98.2	" 5	46.70	98.3
" 27	99.30	97.5	" 18	114.20	100.0	" 8	47.50	100.0
July 1	101.30	99.5						
" 4	101.80	100.0						

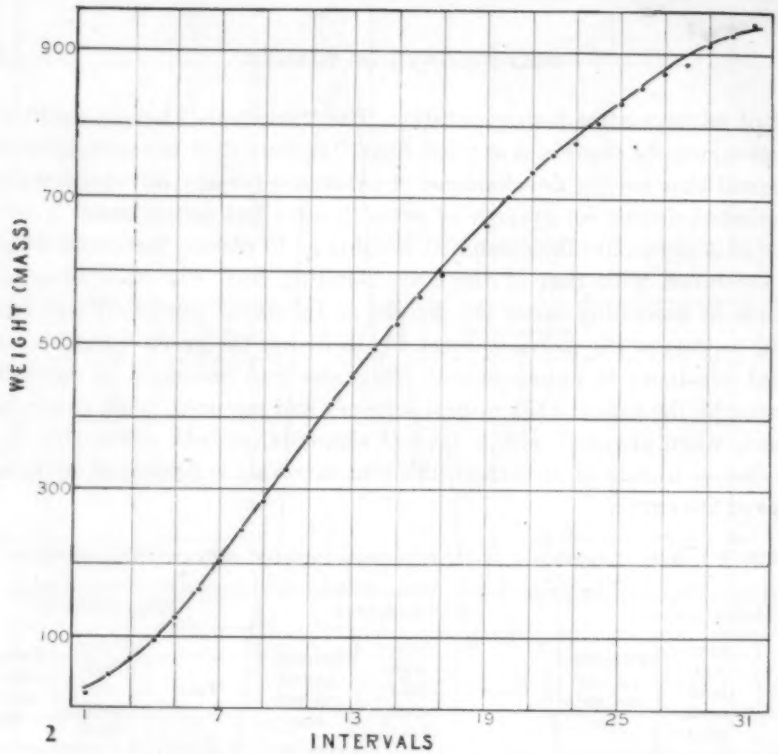
A growth curve of very similar form (fig. 3) was secured by use of other plants from which to plot, according to the usual procedure, progressive change in height against elapsed time.

A series of successive measurements was made to determine the growth rate of leaves of Izmir tobacco. These measurements involved 15 leaves from each of three stalk positions, the basal, median, and upper regions. The data from these measurements are assembled in table 1.

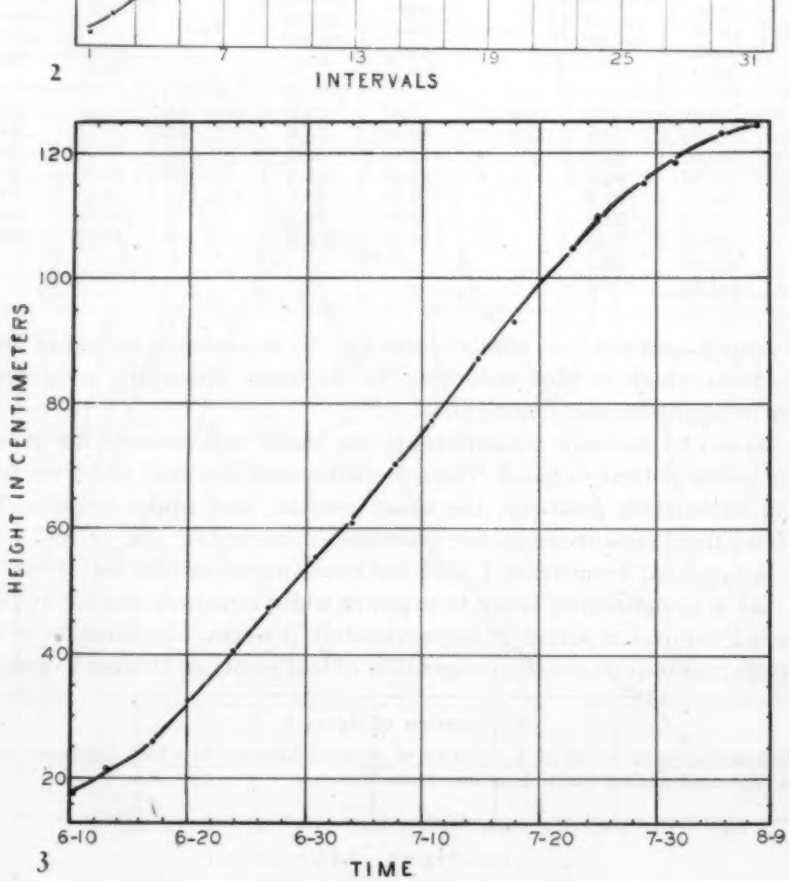
It is apparent from table 1 that the development of the leaf from the time that it is sufficiently large to measure while attached, until it is fully expanded requires a period of approximately 3 weeks, i.e. duration of the growth period is quite constant regardless of leaf position. It must be remem-

Explanation of figure 1

Growth curves of stems of 4 varieties of oriental tobacco, in which internode green weight is plotted against position of internode.

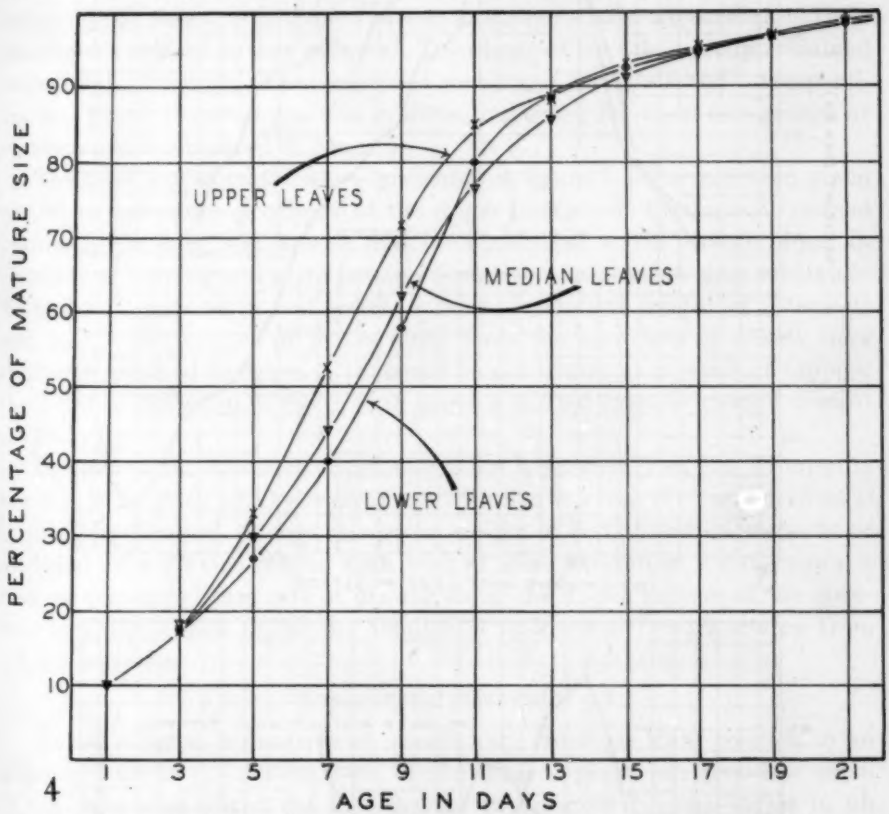

900
700
500
300
100
WEIGHT (MASS)
1
7
13
19
25
31
INTERVALS

2


120
100
80
60
40
20
HEIGHT IN CENTIMETERS
6-10
6-20
6-30
7-10
7-20
7-30
8-9
TIME

3

bered, however, that leaves are not prime, hence are not ready to harvest as soon as they are fully expanded. But the leaves in the median position are the largest, hence their absolute growth rate, called "intensity of growth" by Berthold (1929), is greatest. These data in table 1, however, fail to show the relative rate of growth of leaves borne at different stalk positions. By relative



4

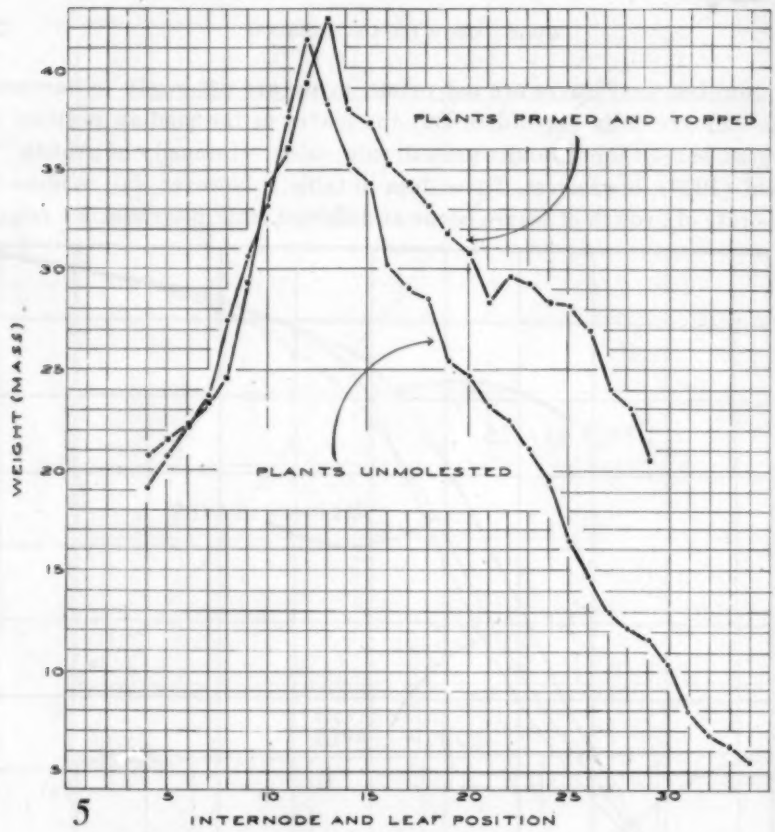
FIG. 4. Sigmoidal growth curves (calculated) showing similarity in rate and duration of expansion of leaves of Izmir tobacco at three stalk positions.

rate is meant herein the percentage daily expansion based on final size. Consequently relative rates of growth were calculated from the observed rates, with the results shown in figure 4.

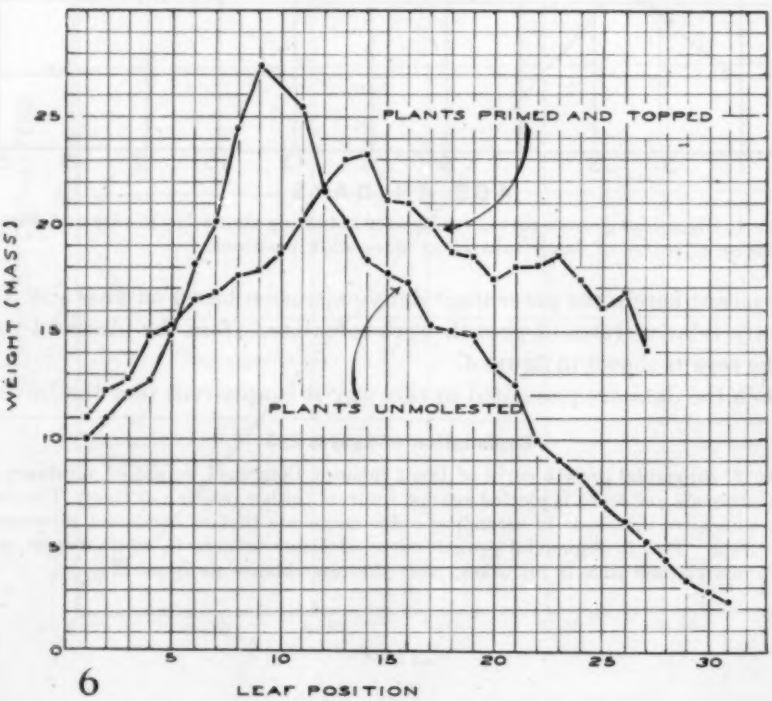
When the data are presented in this way it is apparent that the leaves at

Explanation of figures 2, 3

FIG. 2. Sigmoidal growth curve of Izmir tobacco. Combined weight of substance produced (internode and leaf) is plotted against interval (either position or time). The weight of each successive internode in ascending order augments that of combined substance at a lower level. FIG. 3. Sigmoidal growth curve of Izmir tobacco in which height is one ordinate and elapsed time is the other. Note the resemblance to figure 2.


PLANTS PRIMED AND TOPPED
PLANTS UNMOLESTED
WEIGHT (MASS)
INTERNODE AND LEAF POSITION
40
35
30
25
20
15
10
5
5
10
15
20
25
30

5


PLANTS PRIMED AND TOPPED
PLANTS UNMOLESTED
WEIGHT (MASS)
LEAF POSITION
25
20
15
10
5
0
5
10
15
20
25
30

6

each stalk position exhibit strikingly similar growth rates. The minor differences shown may be assumed to be attributable to differences in weather prevailing during their expansion.

In quest of a correlated cause for change in rate of growth, comparative measurements were made of two groups of plants of the Izmir variety. In one group all plants were topped as soon as the floral-axis appeared, and their leaves were primed as they matured. The plants of the other group remained unmolested. Averages of the combined weights of internode and corresponding leaf plotted against position in ascending order for these two groups of plants may be compared in figure 5.

The most noteworthy feature presented in figure 5 is the increased green weight of substance produced at the upper portion of the topped, primed plants. It has long been known that the uppermost leaves become larger in response to topping and there is coincidentally an increase in stem substance. To isolate "increase in leaf weight" from "combined weight of internode and leaf," the weights of leaves alone from the same sets of plants were similarly graphed in figure 6. It should be noted that as a result of topping the point of inflection of the growth curve is shifted farther upward toward the stem tip.

In figure 6 the influence of priming is not separated from that of topping but it may be presumed by comparison with figure 5 that the greater effect is induced by topping. At any rate green weight of leaf substance seems to be modified to a greater degree than that of stem substance. Furthermore it may be concluded that rate of growth along the upper portion of the stem-axis is accomplished under the dominance of internal factors arising from the inflorescence.

INTERPRETIVE DISCUSSION

As anticipated, a gradient of growth rate from one stalk position to an adjacent one in the development of the tobacco plant was found to exist. When otherwise stated the growth rate in different regions varies in an orderly way, so that increase in green weight plotted against position yields a sigmoidal curve. For best growth of oriental types of tobacco, experience has shown that growth rates should be slow and uniform from the time the plants become established after transplanting until the end of harvesting. Under ideal conditions, therefore, for this crop, the characteristic growth

Explanation of figures 5, 6

FIG. 5. Comparison of distributional growth curves of Izmir tobacco. One group of plants was topped and primed and the other was allowed to grow unmolested. Weight of internode and leaf combined is plotted against position. The weight increases progressively to a point of inflection at the median region and then it decreases progressively. FIG. 6. Comparison of distributional growth curves of leaves only of Izmir tobacco, otherwise as in figure 5. Vegetativeness is increased in response to topping and priming.

curve should approximate a straight line. At least two factors are involved in securing the degree of uniformity in growth rate shown herein. They are (a) the use of organic fertilizer instead of inorganic materials for the purpose of making nutrients slowly available, and (b) the selection for use as seed plants of those individuals that flower and fruit late, thereby tending to promote a long growth period. At present it seems doubtful whether it is practical further to modify the growth rate and thus to improve the quality of oriental tobacco or further to straighten the curves of growth shown in figures 2 and 3.

It is well known that the increments by which weight increases during growth are related to the weight of the organic mass producing these increments. Various investigators, recognizing the existence of this ratio "increment/mass" $\frac{(\Delta m)}{m}$ have attempted to express mathematically increase in assimilatory power or "net assimilation rate" (Williams 1946). For instance, Blackman (1919) likened such continual augmentation to money increasing at compound interest. He employed the equation $W_1 = W_0 e^{rt}$, where W_1 = final weight, W_0 = initial weight, t = time, and r, used exponentially, the rate at which material present produces new substance. Hence e^{rt} becomes the efficiency index. The similarity between growth and compound interest does not hold throughout the entire developmental period, however, as indicated by Glaser (1938), for the reason that, as time goes on, percentage production declines and eventually stops.

Other investigators, including Bernard, Chodat, Loeb, Robertson,[3] Hatai (1911) and Reed (1921) have considered rate of growth analogous to autocatalytic reaction, and in certain instances (Reed & Holland 1919) actual curves of growth have been compared with calculated (autocatalytic) curves. They assumed that growth rate is analogous to the velocity of a monomolecular autocatalytic reaction; or $V = \frac{dx}{dt} = k(a-x)$, where V = velocity of reaction, x = size of the organism at time t, and a = final size. But as x increases, the new substance produced also exercises a catalytic effect, hence $\frac{dx}{dt} = k'x \times (a-x)$. By integrating, Pearl and Reed (1923) derived $\frac{1}{at}\log\frac{ax}{a-x} = k'$. When the organism is half grown $(a/2)$, and hence when the reaction is half completed (duration being considered t'), by integrating, $\log\frac{x}{a-x} = K(t-t')$. If this formula is applied to epochs in organic growth, the observed and calculated growth curves exhibit a high degree of "closeness of fit." Such mathematical treatment appears, however, to have a limited use-

[3] See Thompson, l.c., pp. 256–258.

fulness when applied to total growth and, as Thompson (1945, p. 261) has emphasized, the *modus operandi* of growth still remains unexplained.

As shown in figure 2, the green weight of substance produced increases progressively from the base of the stalk to the median stalk region, and then there is a progressive decrease. A similar relation between length of internode and position exists, as might be expected, although it is not shown, and if length is plotted against position the result is a sigmoidal curve.

To express growth in the manner employed in figure 2, in preference to plotting elapsed time against either green weight, dry weight, or height, does not conform with the usual procedure. No single method of expressing growth seems entirely adequate and all are open to criticism. One reason for this situation is that the moisture content of leaves, and presumably of internodes also, is known to differ at different stalk positions, the uppermost leaves containing the larger proportion of dry substance (Wolf & Jones 1944). Williams (1946), who studied the growth of *Phalaris tuberosa* L., concluded that during early vegetative development leaf area and leaf weight are satisfactory indices of growth but, all in all, amount of elaborated leaf protein is the more adequate index.

As regards responses induced by topping, Avery (1934) demonstrated that increased leaf size in topped tobacco plants was not due primarily to production of new cells but to increase in volume of cells already present. Petrie, Watson and Ward (1939) concluded that when plants are topped, shifts in leaf area and in dry weight, that tend toward counter-balance, are induced. They expressed the opinion that assimilates destined to produce the inflorescence in non-topped tobacco plants either remained in the leaves of topped plants or a portion of the food was translocated to the roots. Increased leaf size, induced by topping, was explained by Wolf and Jones (1944), as a compensatory response, tending to follow Le Chatélier's Law.

The present observations on rate of leaf expansion and on the duration of growth are opposed to generally accepted beliefs as expressed by Wolf and Jones (1944) and they do not confirm the findings of Berthold (1929)[4] with tobacco. The lack of accord on these matters may most reasonably be ascribed to the fact that leaves are not ready to harvest as soon as they attain mature size. But there remains the probability that differences in cultural practices with different types to tobacco may account for differences in rate and duration of leaf expansion.

Thompson (1945, p. 281) states that "we are at present little able to explain the characteristic form of the growth curve but for it we may hope

[4] Berthold, T., l.c., p. 55. "Die Wachstumsdauer der unteren Blätter der Pflanze ist am kürzesten. Mit zunehmender Insertionshöhe bis zu den mittleren Blättern verlängert sie sich. Zwischen den oberen und mittleren Blättern ist der Unterschied in der Länge des Wachstums meistens klein."

to have some day a simple explanation." The fact, as shown in figures 5 and 6, that a shift in the curve, consequently a change in slope, can be induced by the removal of the floral-axis (topping) appears worthy of consideration in connection with this conclusion. The present observations leave no doubt that the change from an increasing to a decreasing velocity of growth of the tobacco plant is initiated by and controlled by mechanisms that attend the development of the flowers and seed pods. The primary causes are presumably hormonal, are produced by the tissues of the floral-axis, and these hormonal substances tend to inhibit "vegetativeness." Such interpretation assumes that the factors which regulate vegetativeness also are hormonal. From these assumptions it follows that the point of inflection of the differential curves in figures 5 and 6 marks the period of occurrence in the plant's development of an hormonal balance between "vegetativeness" and "reproductiveness." A small degree of support for this interpretation arises from observations like those of Priestley and Pearsall (1922), who noted in studies of growth of roots of *Tradescantia zebrina* Hort. and tomato that decrease in velocity of growth is coordinated with the initiation of lateral meristems.

On the other hand, the flowering and fruiting of plants has been explained on the basis of a change in nutritive balance. It has long been known that the change from a vegetative phase or condition to a reproductive one is accompanied by a change in carbohydrate/nitrogen balance. Fisher (1916), for example, reported that vegetativeness is characterized by a carbohydrate content that is relatively low in proportion to the nitrogen content (i.e. there exists a low carbohydrate/nitrogen ratio), whereas the ratio is high when plants are in the reproductive condition. Corroborative evidence of such change in equilibrium has been found to occur in tomato (Kraus & Kraybill 1918) and in wheat (Hicks 1928). There are some who interpret such change in carbohydrate/nitrogen ratio as the proximate cause of flowering, whereas others regard it as a more distally related factor in a concatenation of causes and effects. The interpretation of the latter group is strengthened by the fact that the carbohydrate/nitrogen ratio may not be uniform throughout the entire plant (Hicks 1938, Darkis et al. 1936). Quite commonly the samples used for analysis in appraising carbohydrate/nitrogen ratio have consisted of an aliquot from a composite of the entire plant rather than of particular parts or organs. When the samples are thus prepared the fact that chemical differences exist between organs or that such differences may be localized within an organ are quite completely obscured. This situation is shown in a striking manner by Andreadis et al. (1939) in their findings on the distribution of nicotine in the leaf of tobacco. They found that nicotine increases progressively from the base to the tip of the leaf, from the midrib to the leaf margin, and from the secondary veins toward the parenchyma tissues

most distant from these veins. These differences were of the order of twice to three times as much in one locus as in another.

In the light of the varied approaches that have been made to problems of growth of cells, tissues, organs, or of the ontogenetic development of any organisms in its entirety, and to the interpretations of such studies, it becomes axiomatic that growth is not to be regarded as a simple process, but as a complex of interdependent processes. There is little likelihood, therefore, that by means of a simple explanation, as some investigators believe, growth curves will come to be adequately understood. Rather it should become increasingly apparent upon reflection that, at least for the present, botanists should devote themselves to fundamental considerations of growth whether of roots, stems, leaves, flowers, or fruits, for by so doing they will contribute to a better knowledge of these growth complexes, and, as a consequence, it may become possible eventually to synthesize a broad, integrated growth principle or set of principles.

The change in absolute velocity of growth near the median stalk region may also be basic to the primary grading or classification of cured tobaccos into the two grades "lug" and "leaf." Lug grades of flue-cured tobacco are produced along the lower half of the stalk and leaf grades along the upper half, with some degree of overlapping in position occasioned by seasonal differences. The fundamental differences between these two grades are not believed, however, to be causally determined by environment but by internal factors. Leaves belonging to the lug grade arise under the dominance of internal factors governing vegetativeness and those to the leaf grades under the dominance of internal factors governing reproductiveness. These two groups of factors are not additive or augmentative in conditioning rate of growth but instead have a subtractive or oppositional effect.

The designations "lug" and "leaf" have been established for a long time among tobacconists. How and why they were introduced is controversial, and no real purpose is served at this time by statement or opinions pertaining to this subject. The fact remains, however, that there are chemical differences in composition between leaves of these two grades, and between leaves of their subdivisions, in the case of flue-cured tobacco, as shown by Darkis et al. (1936). These chemical differences, to be sure, reflect metabolic or physiologic differences during growth and maturation.

The straight portion of the curve, as regards oriental tobacco, is clearly all-important. Further increase in the production of quality grades of oriental types of tobacco would seem to be related to modification of cultural practices in such manner that rate of growth could be expressed as a curve that approximates through its entire length a straight line. To do this vegetativeness should be enhanced at the expense of reproductiveness. If this procedural approach is the correct one, then the "lug" zone might be further

extended, as should result, if flowering were delayed until essentially all the leaves had been primed.

If the critical point of inflection in the growth curve of tobacco is related to vegetativeness as opposed to reproductiveness, then for the first time a rather simple explanation is at hand for the characteristic growth curve of this species, and also for the first time there is established a morphologic basis for the primary grading of cured tobaccos.

These observations on growth of oriental types of tobacco also suggest that growth curves might become useful aids in determining the extent to which quality and yield of tobacco of any type may be modified by different topping practices, by spacing, by the application of fertilizers, or by other cultural practices.

SUMMARY

A study has been made of the rate of growth in oriental types of tobacco. As anticipated, mass plotted against time is found to yield a characteristic sigmoidal growth curve, but mass plotted against stalk position yields a distribution curve with a maximum in the median stalk region. The rate of growth of the stems or of expansion of the leaves when plotted against time also becomes a sigmoidal curve.

The duration of the period of expansion of leaves borne at different stalk positions is quite alike. Rates of leaf expansion, irrespective of leaf position, when based on final size, are also quite alike.

Removal of the floral-axis (topping) induces a change in slope of the growth curves as a result of disturbance of balance between the hormonal complex that controls vegetativeness and the complex that controls reproductiveness.

The inflection of the growth curve at the median stalk position is interpreted as being causally related to opposition between the hormonal factors that control vegetativeness and those that control reproductiveness.

On the basis of such interpretation the leaves produced under the dominance of vegetativeness are in the "lug" grades, and under the dominance of reproductiveness, in the "leaf" grades. The proportion of lug and leaf grades and their quality are therefore, to a degree, controllable by cultural practices.

It is suggested that growth curves might serve to aid in the interpretation of results of various agronomic practices with tobacco.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 3, pp. 215–231 MAY, 1947

A PHYSICAL ANALYSIS OF GROWTH AND STRUCTURE OF SOME GRASSES

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An expanding phenomenon in time is usually associated with organic growth. As a first step there is the formation of new protoplasm, which is always accompanied or immediately followed by a permanent increase in the amount of non-living materials. Hence the growth of a plant consists primarily in the formation of new cells, of their enlargement and specialization, so that "a quantity of growth" implies more than a simple progressive increase in size with an accompanying increase in mass, or decrease in density. Accompanying the physical changes in form and structure must be changes in internal stresses, which must manifest themselves as variations in the elastic constants of the material as the structure develops.

In the growth process each section of the plant, in its development, has its formative stage, its elongative stage or "grand period of growth," and its stage of maturation. These dynamic aspects of the growth processes have been analyzed in great detail and with Buchanan (1) we may divide the whole period of growth into (a) a lag phase, (b) the phase of logarithmic increase, (c) the phase of retardation, (d) the stationary phase plus the alternate terminal phase of restoration (e), or decline (f).

These phenomena constitute the generalized interpretation of a typical sigmoid growth curve usually expressed in terms of length or mass units as the dependent variable (green weight, dry weight, or height) plotted on the y-axis, and time as the independent variable plotted on the x-axis. In general, if the total increment of growth is plotted against time, the resulting curve will be sigmoid in shape. On graphically differentiating such a sigmoid-shaped curve and then plotting the differential values as a function of time one obtains an asymmetric distribution curve, showing the increase in height, green weight, or size of leaves along the stalk of a plant, in terms of increments of time. The ascending phase of this distribution curve will be steeper than its descending phase. If, however, the sigmoid-shaped curve is symmetrical (S-shaped) so that the point of inflection, where the change from an increasing to a decreasing velocity of growth is indicated, lies halfway up the curve, then the distribution curve is also symmetrical and approaches the form of the bell-shaped probability curve.

Conversely, if a distribution of length, mass, volume or any other physical characteristic of a completed structure, in the form of a mature plant, is graphically represented in terms of any independent variable, it should

be possible to obtain from such data a growth-characteristic of that plant. Graphically integrating such a distribution curve will reduce it to a sigmoid-shaped growth curve, if the distribution curve is asymmetric, or to the S-shaped counterpart if the distribution curve is symmetrical.

The object of the analysis of grasses that follows is to show that the static physical or structural characteristics of a mature plant, after it has attained its "stationary phase," can be used to obtain certain physical growth characteristics, providing the physical measurements can be represented as a distribution curve, when the distribution is independent of the time element usually associated with a "quantity of growth."

Analysis of Arundo donax. One of the most stately of the ornamental grasses found in the southern United States is the giant reed (*Arundo donax*), often reaching a height of 20 feet or more, and topped with a gorgeous green-gray tassel. This giant reed is a member of the *Class Monocotyledones*. The most prominent physical feature of its slender stalk is its segmental division into a large number of tubular joints (internodes) between stiff circular nodes. During growth the elongation of the internodes takes place at their bases where they contact the nodes and the base of the sheaths which surround the cylindrical internodes.

On examining a very tall mature reed, one is struck by the architectural effects of the distribution of its nodes along the stem. The internodes are very short at the base, increase in length as we ascend the stem, and reach a maximum length at a point about one fourth of the way up the structure. This characteristic increase in length is followed by a distribution in which the internodes are progressively shorter until they terminate in an enormously elongated floral-axis surmounted by the tassel.

In this ascending distribution of change in the physical characteristics of the internodes we have a static, but complete picture, of a phase of "exponential increase," followed by the static structure reflecting a phase of retardation.

Figure 1 shows typical variations in the length of the internodes of *Arundo donax* in terms of the ascending position of the internodes along the stem. The data represent arbitrary samples taken from the same patch of grasses during each of three consecutive years. We immediately note that the lengths of the internodes diverge more rapidly in the lower segment (phase of exponential increase) than they converge in the upper segment (phase of retardation). The discontinuity between the sequences is localized at the maximum of this distribution-in-length curve, which is usually found to be associated with the center of gravity of the reed, and will be referred to as the *critical point* or inflection point of the stem.

If we determine the dry or green weight of the internodes with or with-

out attached leaves, and then graphically represent the green weight of the internodes and leaves, in terms of their ascending order, we obtain similar asymmetrical distribution curves, as shown in figure 2. They all indicate that the maximum length, mass, or volume (fig. 3), for any given stem, is always a common attribute of the same node lying at the *critical point* or point of inflection on the sigmoid growth curve.

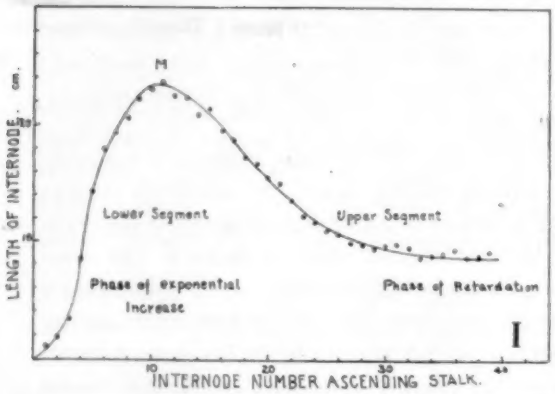
If we plot the total increment of length, of the same stem, as a function of the position of the internodes in ascending order, we obtain a typical sigmoid curve, as shown in figure 4, whose point of inflection coincides with the maximum (critical point) of the distribution curve of figure 1. The same type of sigmoid curve is obtained if a distribution curve of the form shown in figure 3 is graphically integrated, as shown by the broken curve in the same figure. Figure 3 illustrates the changes in volume of the hollow internodes of *Arundo donax* in terms of the positional number of the internodes in ascending order, up the stem.

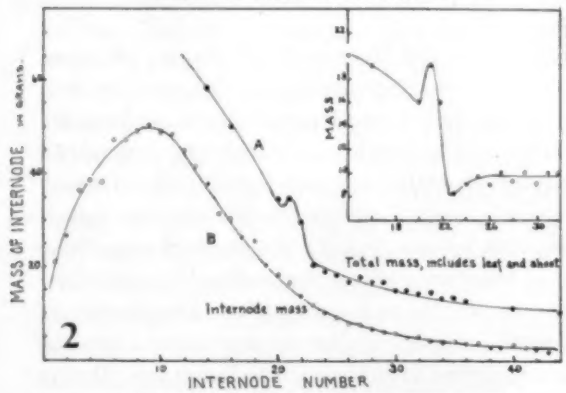
If the form of the sigmoid curve, showing the variation of some physical factor as a function of time, is accepted as representing the dynamic growth characteristic in time, it should follow that if an identical graph is obtained by integrating a curve representing a distribution in which the dependent variable (y-axis), is the same physical quantity as represented in the sigmoid curve, then the independent variable (x-axis) used in the distribution curve must be a function of time. In this way we may justify the use of the position of the internode, or distribution of substance along the stem as the independent variable, provided we limit the results to a qualitative interpretation.

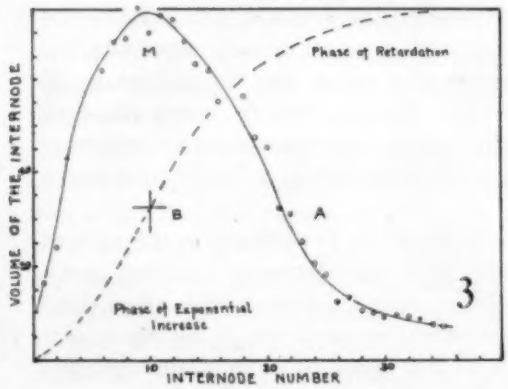
Thus a curve depicting the mass, length, volume or any other physical characteristic distribution, in a completed static structure (mature plant), as a function of the position of the internodes, the graph should indicate the same growth characteristics as its comparable sigmoid growth curve (fig. 3).

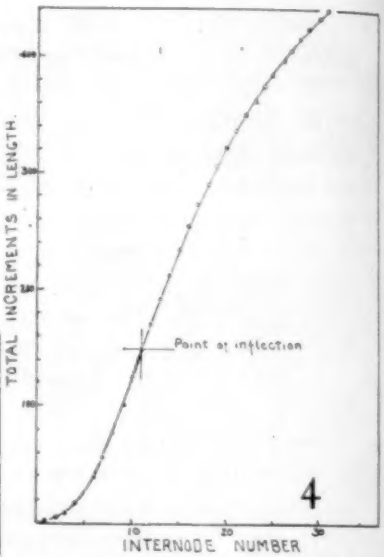
Presentation of the data as a distribution curve has the advantage of showing more precisely where the growth changes from its major phase of exponential increase to its phase of retardation. Any irregularities occurring in either growth phase are also more easily identified in a distribution curve than in a sigmoid growth curve.

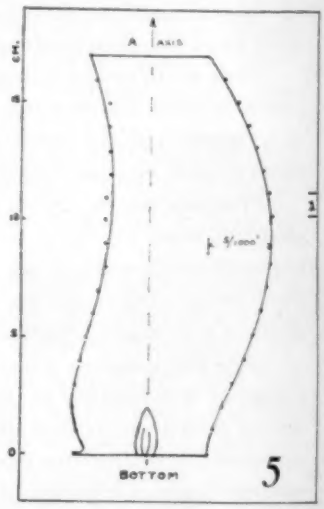
Note for instance what appear to be irregular departures in the normal phase of retardation of the total mass of internodes with attached green leaves shown in curve A of figure 2. The enlarged insertion shows how these apparent irregularities near the twenty-first internode are in realify a local change from the phase of retardation to a phase of exponential increase followed by an appreciable compensation of greater retardation in the immediately following group of higher internodes. Such sudden changes in slope were always found associated with the presence of a bud or branch. Apparently such changes in slope must be attributable to the development


M
Lower Segment
Upper Segment
Phase of exponential increase
Phase of Retardation
LENGTH OF INTERNODE cm.
INTERNODE NUMBER ASCENDING STALK.
1


A
B
MASS
Total mass, includes leaf and sheat
Internode mass
MASS OF INTERNODE in grams.
INTERNODE NUMBER
2


M
Phase of Retardation
B
A
Phase of Exponential Increase
VOLUME OF THE INTERNODE
INTERNODE NUMBER
3


Point of inflection
TOTAL INCREMENTS IN LENGTH.
INTERNODE NUMBER
4


A Axis
cm.
BOTTOM
5

of a secondary structure on the main stalk. The secondary structure apparently uses part of the available energy for its own growth, thus changing the rate of growth in subsequent higher internodes and their attached leaves.

In support of this view may be cited the critical analysis of "the compound interest law and plant growth" by Blackman (2), who pointed out that the reproductive development usually occurred during the period of deceleration in rate of increase in dry weight. The observations of Priestley and Pearsall (3), indicated that the decrease in the velocity of growth of the roots of *Tradescantia zebrina* Hort. and tomato could be coordinated with the initiation of lateral meristems. Pearsall (4) in his studies of the growth of cotton also attributed the decreased rate of growth of the stem to flowering.

If the development of a bud or branch can cause local changes in the slope of the growth curve, it should follow that the predominant change in slope identified with the *critical point* located by the maxima of the distribution curves, should be attributed to similar but more fundamental internal changes in the plant structure.

Euler's Column Theory Applied to Internodes. If the foregoing hypothesis is biologically acceptable it should follow that radical changes in the internal composition and structure of the stem, as reflected by changes in the elastic modulus of the material, should be found associated with those internodes which lie at the maxima of the length, volume, and mass distribution curves.

To explore the possible changes in internal structure of the nodes along the stalk two structural tests were applied involving the modulus of rigidity of the material. The first involved examining the internode as a unit column, placing it under a compression load until fracture took place. The second,

Explanation of figures 1–5

FIG. 1. A distribution curve showing typical variations in lengths of the internodes of *Arundo donax* in terms of the ascending position of the internodes. *M*, the maximum, is the point of inflection of the equivalent sigmoid growth curve. FIG. 2. A distribution curve showing typical variations in mass of the internodes of *Arundo donax*. A, shows variations in total green weight, which includes weight of internodes, leaves and any attached buds. B, shows mass of internodes after leaves and buds have been removed. Insert shows in detail the change in slope of graph A, near the twenty-first internode due to the presence of a bud. FIG. 3. A, a distribution of volume of the internode as a function of internode position. B, the graphical integration of curve A produces a typical sigmoid growth curve. Point of inflection B coincides with the maximum of the distribution curve. FIG. 4. A typical sigmoid growth curve obtained by plotting the total increments in length. The measurements were obtained from the same plant that is represented in figure 1 as a distribution-in-length curve. FIG. 5. Contour of the x-axis and y-axis of a 17 cm. internode of *Arundo donax*. The vertical scale shows that measurements were made at centimeter intervals. The horizontal axis is on a scale 1000 times greater than the vertical centimeter scale. The contours have the form taken by an elastic column under compression.

a more rigid and quantitatively interpretable process, involved a determination of the elastic modulus of compression and then the evaluation of the compression modulus in terms of the "slenderness ratio" of the columns. This will give critical internal structural information about the stiffness of the internodes in terms of ratio of length to radius of gyration. From such data we can then draw quantitative conclusions about changes in internal structural properties of the internodes without resorting to the procedure of plotting a distribution curve in terms of the position of the internodes.

It is proposed to examine the internodes under compression and determine whether their yield stresses and their fracture stresses radically change as we pass from the lower segment through the *critical point* to the upper segment of the stem.

The internode-structure closely approaches the form of cylindrical shells. Such a structure when put under compression in the direction of the longitudinal axis will at first bend and then fracture. This type of failure is that investigated by Euler in 1757, who showed that the strength depends on the ratio of length to radius of gyration of the cylindrical shell, and on the modulus of elasticity of the material.

Euler sought, on theoretical grounds, to determine the least value that an axial load P (pounds or kilograms) must attain so that an elastic slender column will start to bend. Since a column buckles when the load is increased only a small amount above this value, then P is also the minimum load that the column can resist, so that the axial compression will make the column fail by buckling and not by crushing. This critical load for an ideal pivot-ended column was shown by Euler to be equal to

$$P = \frac{\pi^2 E I}{l^2}$$

where P is the axial load in pounds, E the elastic modulus of the material expressed in pounds per square inch, I the moment of inertia of the cross-section of the column about the neutral axis, and l its length. If a is taken as the area of the cross-section and r the radius of gyration of the cross-section about the neutral axis, then Euler's column formula may be written

$$\frac{P}{a} = c\frac{\pi^2 E}{\left(\frac{l}{r}\right)^2}$$

where l/r is called the slenderness ratio of the column, and c is a constant depending on the end conditions of the cylinder when the pressures are applied.

From Euler's equation we may expect P/a to be inversely proportional to the square of the slenderness ratio, $(l/r)^2$. By an increase in slenderness can be meant (a) an increase in l with r constant, (b) a decrease in r with l constant, (c) or an increase in l and a decrease in r.

These theoretical results show that the only internal property of the material on which P depends is E, the modulus of elasticity, or stiffness (not rigidity) of the material. Since the idealized end-conditions cannot be reproduced with plant structures as successfully as in the supports of columns used in engineering practice, and since the complexity of the fiber-structure of the shaft of the reed must certainly be taken into consideration, one can expect only limited agreement between an ideal cylindrical column and actual cylindrical plant structures.

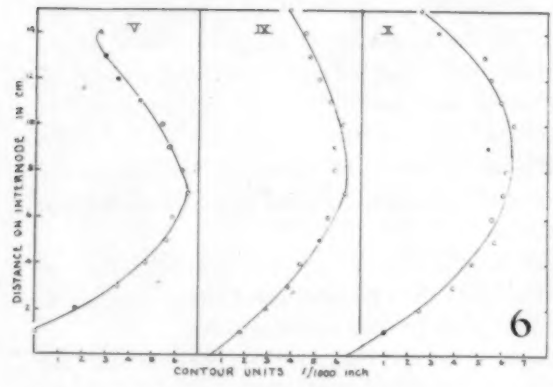
The first object is to determine to what extent the external structure of the internodes of *Arundo donax* resemble the idealized mechanical configuration of a uniform cylindrical column with proper end supports.

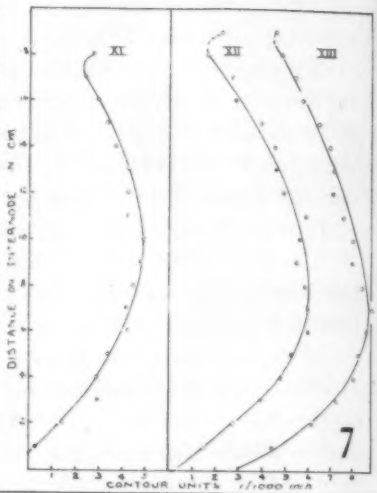
If an internode is to be used as an ideal test-column then the external and internal radii must be constant throughout its length. The external contour of the internodes were therefore explored by means of a sensitive spring gauge, which was calibrated to read 1/1000 inch. The internal radius was explored by measuring the thickness with a screw gauge. To determine the degree of departure from a round column the internodes were mounted on a plane steel surface, and the change in height along a geometrical longitudinal axis was measured at centimeter intervals. The internode was then rotated to a 90°, 180°, and 270° position and variations in contour were also determined along these longitudinal axes. For convenience of notation the *A-axis* is taken as the longitudinal line on which the bud is located. The *y-axis* lies 90° anticlockwise, followed by the *B-axis* and *x-axis*, at 90° intervals. Figure 5 shows a typical series of contour measurements along the x and *y-axes* of an internode. This form of contour is typical of most of the longer internodes. The contours are typical harmonic curves, similar to those developed by elastic metal columns subjected to compressional forces. The internode, during its growth, seems to have been subjected to longitudinal stresses which in effect act as a deterrent to prevent the column from being perfectly cylindrical, or the leaf at the node seems to have acted as a circular constrictor to produce these mathematically correct distortions.

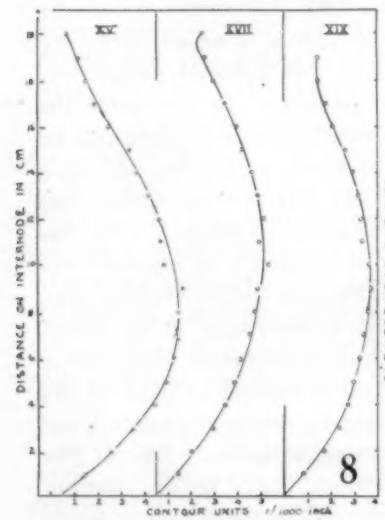
The over-all shape is very nearly cylindrical, as one can see from figure 5 where the length is plotted in terms of centimeter intervals and the change in contour in 1/1000 inch units. The maximum over-all departure of this 17 cm. long internode, from a true cylindrical column, is a bulge of 5/1000 inch located near its midpoint.

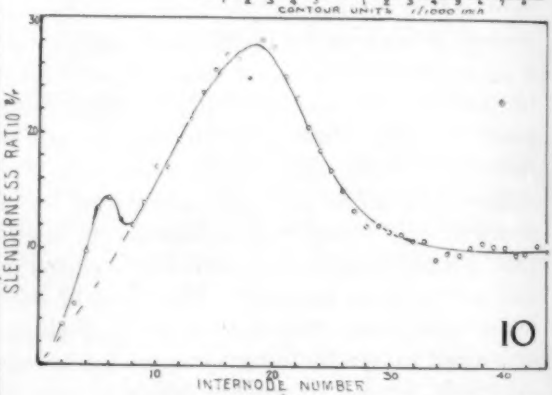
Figures 6, 7, 8, and 9 show how thirty-eight successive internode-contours progressively change as we ascend the stem. The long internodes of *Arundo donax* lying above and below the *critical point*, that were subsequently examined, never departed more than 6/1000 inch from true cylinders, a variation of not more than ¼% from a true circular column.

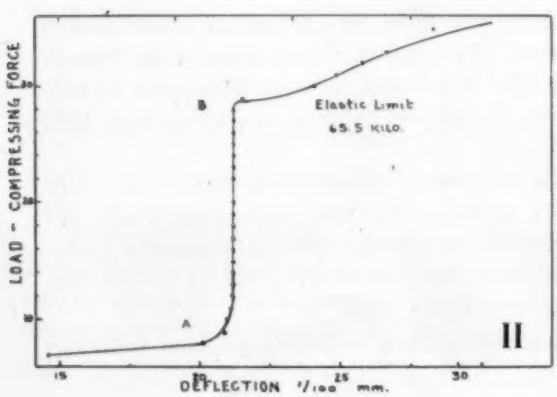
To a fair degree of approximation we can therefore proceed with the

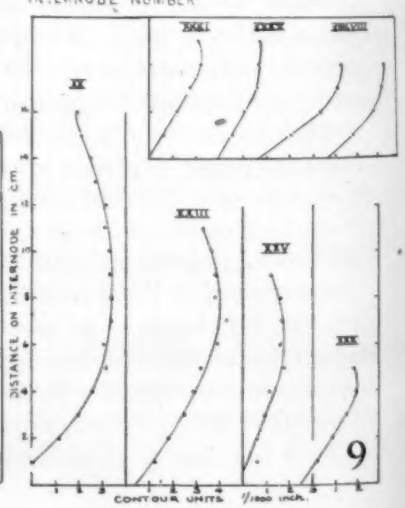

V
IX
X
DISTANCE ON INTERNODE IN CM.
CONTOUR UNITS 1/1000 inch
6


XI
XII
XIII
DISTANCE ON INTERNODE IN CM.
CONTOUR UNITS 1/1000 inch
7


XV
XVII
XIX
DISTANCE ON INTERNODE IN CM.
CONTOUR UNITS 1/1000 inch
8


SLENDERNESS RATIO %
INTERNODE NUMBER
10


LOAD - COMPRESSING FORCE
B
Elastic Limit
65.5 KILO.
A
DEFLECTION 1/100 mm.
11


XXI
XXV
XXVIII
XX
XXIII
XXV
XXX
DISTANCE ON INTERNODE IN CM.
CONTOUR UNITS 1/1000 inch.
9

compression tests assuming that the middle half section of an internode may be treated as if it were a hollow cylinder conforming nearly to Euler's ideal cylindrical contour.

Fracture Tests. Values of the slenderness ratio, l/r, were next measured and identified with the internode position along the stalk. Here l represents the distance between two consecutive nodes and r the radius of gyration, i.e. $\left(\frac{(R_i)^2+(R_e)^2}{2}\right)^{\frac{1}{2}}$ where R_i and R_e are the internal and external radii respectively. Typical results are shown in figure 10. The lower segment shows that the slenderness ratio increases as we ascend the stem, attains a maximum at the same *critical point* as the other physical factors and then decreases less rapidly in magnitude toward the top. This verifies the assumption that the stem, considered as a unit structure, is also characteristically divisible into two segments having very different internal structural characteristics.

In order to explore this possible internal structural difference, the stems were cut into cylinders with a node at each end. Under these circumstances only every other internode could be examined. By this method nearly similar nodal end supports to all the columns were provided. Such columns were examined for ultimate strength (breaking load per original cross-section area) with a testing machine whose compressional force could be increased in 2-pound steps.

Ultimate strength is defined as the greatest unit stress that the column can stand in compression without breaking. This is designated as P/a where P is the load in pounds and a the cross-sectional area of the hollow cylinder in square inches.

The results were unsatisfactory because of the limited amount of data available from any one stalk, since alternate internodes had to be discarded. Much of the data was also found to be unreliable because of the great scatter of the points, but general trends were thus established. Later it was noted that the presence of lateral buds introduced large experimental errors. Another difficulty arose for the reason that the measurements could not be

Explanation of figures 6–11

FIGS. 6, 7, 8, 9. These graphs show the progressive change in shape of the right hand vertical contour (fig. 5) of seventeen of the thirty-eight internodes of a tall stem of *Arundo donax*. Note that the contours of the enumerated internodes bulge less as we ascend the stem. They simulate the physical appearances of a cylindrical rod under pressure, responding to a progressive decrease in vertical load. FIG. 10. The slenderness ratio (l/r) of length to radius of gyration of the hollow cylindrical section of the internode is shown to have the form of a typical distribution curve. The departure from the smooth curve near the origin is due to the influence of a large bud. FIG. 11. A typical graph showing the progress of the flexure of a longitudinal axis of an internode of *Arundo donax* under compressional test. B is the yield point. In this sample, fracture occurred when a load of 65.5 kilograms was applied.

repeated, due to the destruction of the material on fracture. In general, however, the trend of the data indicated that the lower segment always showed a decrease in ultimate strength with increase in slenderness ratio while the upper segment showed a decrease in ultimate strength as the slenderness ratio decreased. The stem must therefore be rather stiff at its base, become less stiff as we ascend through the middle third, where it passes through a critical internal structural phase. Here the internode suddenly becomes even more stiff than those at the base and then they progressively become less stiff as we near the upper internodes.

These results again support the assumption that the *critical point* of the distribution curve indicates a unique structural change due to some internal economy of the plant.

From Euler's equation we would expect the fracture tests of the internodes to show that the product $(P/a)(l/r)^2$ is constant, assuming E, the modulus of rigidity, to have the same value for all internodes. The available data showed however that this relation was not constant for all the internodes in any given plant. Under the circumstances it became necessary to determine the modulus of rigidity for every internode as we ascend the stalk to verify the suspicion that the trend in the value of E must change radically at that internode identified with the apex of the distribution curve. This should lead to quantitatively interpretable results from which the internal structural quality of the plant material can be evaluated.

Tests for Modulus of Elasticity. If we start with a simple short solid cylinder and subject it to an end-load having a very slight eccentricity, the short cylinder may be assumed to be in pure compression since its bending action may be neglected. If the cylinder is thought of as becoming longer (more slender) the tendency to bend becomes greater, until in the limiting case the column is so slender that bending or flexure is the only action that need be considered. The contour of the elastic curve that is generated as a result of the compressing force is similar to the shape taken by a slender stick when it is vertically compressed between the palm of one's hand and the ground which supports its lower end. Any slender internode of the reed must bend in a similar manner if subjected to sufficient pressure directed vertically downward.

To determine the magnitude of the modulus of digidity it is necessary to measure the buckling that takes place at right angles to the longitudinal axis of a cylindrical sample cut from the middle section of each succeeding internode. If these hollow cylinders are uniformly compressed in a testing machine, in the axial direction, symmetrical buckling with respect to the axis of the cylinder may start at a certain value of the compressive force which is called the critical load.

A sensitive (1/1000 inch or 1/100 mm.) spring gauge was used to measure the buckled deflection. The graph showing the relation between stress (load in pounds), and the strain (deflection in multiples of 1/100 mm. or 1/1000 inch), is shown in figures 11 and 12. The portion *AB* is a straight line, but *BC* is slightly curved, the lower side being the concave side. The point *B*, at which the strain begins to increase greatly for very little increase of stress, is called the yield point.

Within the portion *AB* of the strain diagram the stress is proportional to the deformation produced, and the material may be considered perfectly elastic. The fact that the experimental values between *A* and *B* can, to a close approximation, be considered as falling on a straight line, shows that within the elastic limit the deformation of the cylinder is proportional to the stress producing it, thus obeying Hooke's law. This can be restated by saying that the ratio of the unit stress to the unit deformation is a constant, and this constant is known as the modulus of elasticity *E*, expressed in lb/in.^{2} or kgm/mm.^{2} Geometrically *E* is the slope of the line *AB* in figure 12.

Figure 13 shows the values of *E* thus obtained from the successive internodes of a single plant (*Arundo donax*) in terms of the height above ground at which the sampling took place.

The modulus of elasticity of the lower internodes was found to be about 1,600,000 lb/in.^{2}, dropping to 400,000 lb/in.^{2} for internodes situated higher up the stalk. These values are of the same order of magnitude as those reported in the U. S. Forestry Circular No. 15 for 32 samples of wood (40% moisture) varying from 2,500,000 for hickory to 910,000 lb/in.^{2} for white cedar. Schwendener (5) reports that the elastic modulus of bast from eight selected monocotylons is on the average about 2,000,000 lb/in.^{2}

Since each successive internode furnished a test-column from which *E*. was determined, the values of *E* could therefore be identified with the position of the internodes in addition to their linear height above the ground. This made it possible to show the correlation between the lengths and position of the internodes and their changing values of *E*. These relations are shown in figure 13, which also shows that the maximum of the distribution-in-length graph coincides with the minimum value of *E* of the elasticity curve.

The measurements indicate that the first internode possesses the greatest modulus of elasticity. As we ascend the stem the modulus of the internodes decreases as the internodes increase in length. The magnitude of the modulus passes through a minimum where the increase in length changes to a regression in length of the internodes. This minimum value of *E* can always be correlated with the *critical points* of the distribution curves.

Of special significance is the secondary decrease in the value of *E*, which was always found when a bud appeared at a node. This is illustrated by the

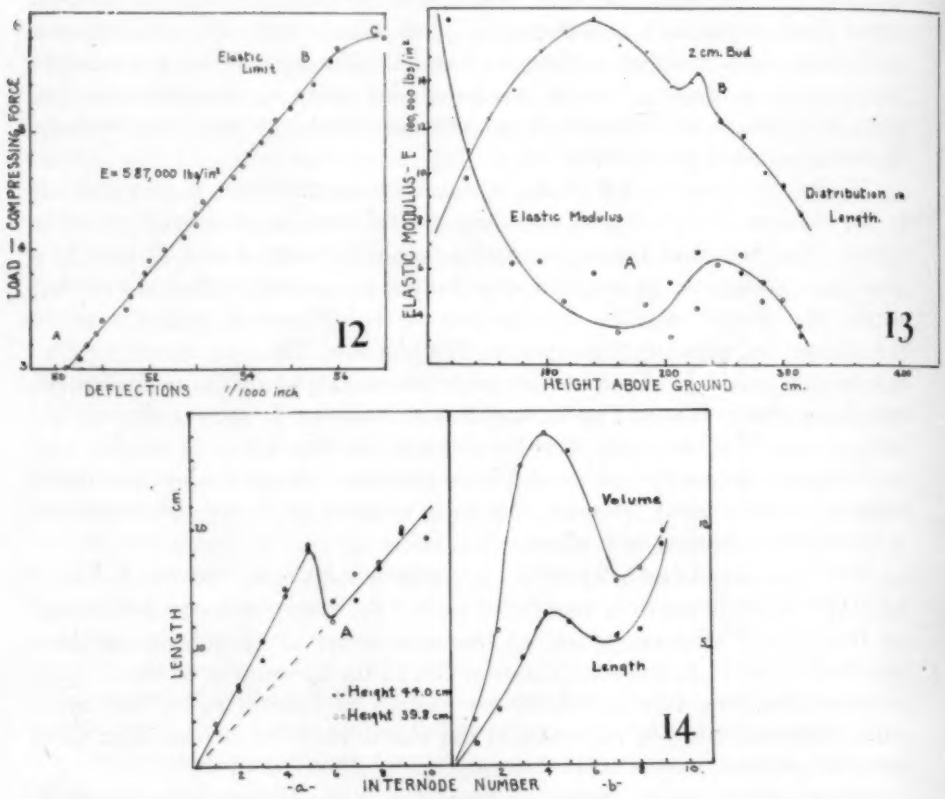


FIG. 12. An example of the flexure produced in a cylindrical test sample taken from the middle section of an internode of *Arundo donax*. Note how closely the data (*AB*) follow the straight line representing Hooke's law. These are not typical data but an illustration of the best results that were obtained from samples cut from the internodes of *Arundo donax*. Beyond the elastic limit *B*, the departure from Hooke's law sets in as shown by *BC*. FIG. 13. Curve A shows the general trend of the values of the elastic modulus *E*. Note that the minimum value of *E* coincides with the maximum value of the length-distribution curve for the same stem. The presence of the 2 cm. bud at *B* is reflected in the elastic modulus curve by the bulge at the sixteenth node. FIG. 14. a. Two nearly equally tall samples of Johnson-grass show identical distribution-in-length curves. The ascending phase of the deceleration in the upper segment at *A* is correlated with the appearance of branches at the sixth and subsequent higher nodes. b. The distribution-in-length and volume curves show identical forms despite the resurgence of growth at the seventh internode.

sudden decrease in E at the sixteenth node, with which a 2 cm. bud was associated. This latter decrease in the value of E shows that the presence of a secondary structure, a lateral bud, reduces the stiffness of subsequent internodes because of modifications in internal physical characteristics, probably brought about by a shunting of some of the food supply into the attached bud.

If the presence of a bud can be correlated with a definite change in the structure, as reflected in the change of the modulus of elasticity, it follows that a much greater change in this elastic constant must indicate a more profound internal change in the structure of the main stem. Such a profound change must therefore be associated with the critical change in the lengths of the internodes, correlated with the minimum of the elastic modulus graph.

From a physical point of view this critical change, at the twelfth node (fig. 13), from a decrease in stiffness to an increase in stiffness must therefore indicate the origin of a change in the internal structure. Since no external structure, aside from the leaf growth, is ever found at this critical position, one might attribute the increase in the value of E to the inception of the floral axis at a node located within this critical region. The subsequent coaxial growth of the stem would then reinforce the structure while draining the food supply to inhibit the growth of the internodes. This situation would account for the increase in the value of the modulus of rigidity (stiffness) of subsequent higher internodes, after which the stiffness factor would again be reduced due to the presence of external secondary growths along the stem.

Those samples which had buds associated with the higher nodes showed recurring decreasing fluctuations in the values of E.

Due to the high elasticity of the material it was often possible to make two consecutive measurements of E at two diametrically opposite places on the cylinder, so that occasionally two values of E could be obtained for the same column. In such instances (fig. 13) the graph was traced through the mean values of E in order to show the general trend of the elastic modulus.

Analysis of Sorghum halepense. In support of these analyses of *Arundo donax* we may examine the structure of Johnson-grass (*Sorghum halepense*).

The samples of Johnson-grass were gathered at random along a one-mile path during July and September. Figures 14a and 14b show the distribution in lengths and volume of samples posessing very few branches. Figure 14 indicates the distribution in length of two nearly equally high grasses picked from a random collection. The uniformity of these samples is shown by the average graph drawn through the mean values of the lengths of the internodes. Figure 14b shows the distribution in length of the internodes as com-

pared with their volumes. Their diameters were measured with a vernier caliper to the nearest tenth millimeter. The distribution is similar to that found for *Arundo donax*, in that the maxima of the length and volume distribution curves are identified with the same internode. The ascent of the accelerating phase is, however, more linear, and neither does the deceleration phase proceed to the top of the stem as in *Arundo donax*, but always passes through a minimum after which a secondary acceleration phase sets in, which terminates in the highest internode. This secondary accelerating growth phase has a smaller slope, i.e. its rate of growth is smaller than the primary growth phase of the lower segment. To a fair approximation both accelerating phases seem to have a common origin, which is located through extrapolation, at the ground level of the plant.

Analysis of Bamboo. That this resurgence in growth activity is not a unique phase confined to the higher internodes of the upper segments of Johnson-grass is illustrated in figure 15, graph A. This shows the distribution-in-length of the internodes in bamboo, as modified by the presence of branches. Here the resurgence takes place in the lower segment. It is correlated with the appearance of the first branches. Yater, it appears again at the node carrying two, and again higher up when the node has associated with it three branches. This is shown in greater detail in the insert of figure 15c where the graph shows how the length of the lower internodes, just emerging from the root, rapidly elongates. With the appearance of a single branch at the seventh internode the length drops to a lower value, indicating the beginning of a slower rate of growth. It seems to indicate that the external growth is dissipating some of the available energy and hence the rate of growth of the stem from this point upward is reduced, as indicated by the change in slope. This critical retardation is also present where the change-over from a one-branch to a two- or a three-branch growth appears at the nodes, as illustrated in graph B of figure 15. The over-all shape of the growth curve of the plant as a whole has, however, not been submerged. It still possesses, despite these superimposed secondary growth phenomena, the fundamental characteristics of the basic distribution curve.

The maximum of the distribution curve is hence indicative of a profound internal structural change, whose existence is not influenced by any secondary growths located either on the ascending accelerating phase, or descending retardation phase of the plant.

Analysis of Arundinaria macrosperma. Similar results are exhibited by the growth curves obtained from southern cane (*Arundinaria macrosperma*).

Without further comment figure 16 is presented to show how the lengths and volumes change with the internode spacing alon- the stem of this cane.

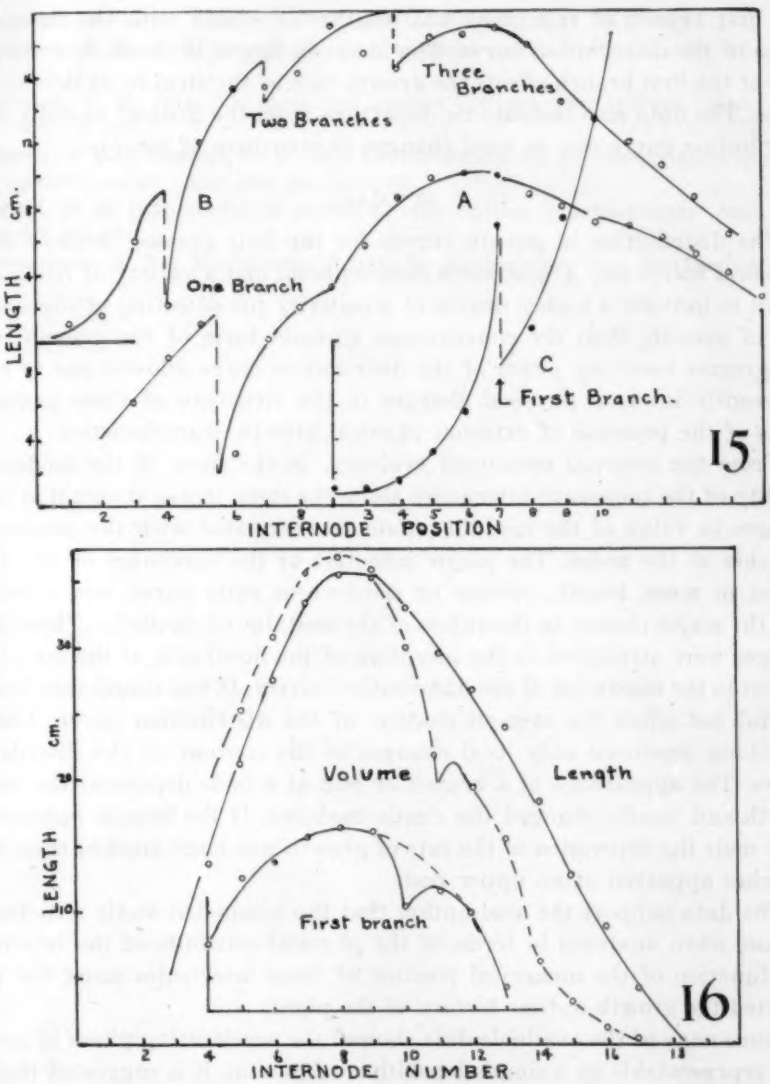


FIG. 15. Distribution-in-length curves for bamboo. A shows how the discontinuity in the ascending phase is correlated with the appearance of branches. Figure 10 shows a similar variation due to the presence of a bud along the stem of *Arundo donax*. B shows how the over-all contour of the distribution curve is maintained despite the variations due to the presence of one, two and eventually three branches per node at the higher node levels. C shows the detailed variation in length due to branching. These data were obtained from three different plants. FIG. 16. An example of the length and volume distribution curves of *Arundinaria macrosperma* with the local effects of branching. Note how the extrapolation of the volume or length curve indicates the maximum or self-limiting number of internodes that can be attained at the close of its growth season.

The first branch of this grass was usually associated with the descending phase of the distribution curve. The insert in figure 16 shows how the presence of the first branch effects the growth rate of the stem in its decelerating phase. The data also indicate no departure from the general contour of the distribution curve due to local changes in structure of the plant.

SUMMARY

The distribution in growth curves for the four grasses, *Arundo donax*, *Sorghum halepense*, *Arundinaria macrosperma* and a variety of bamboo are shown to indicate a higher degree of sensitivity for detecting changes in the rate of growth, than the conventional sigmoid form of the growth curve. The greater resolving power of the distribution curve allowed one to evaluate readily internal physical changes in the structure of these grasses in terms of the presence of external physical growth characteristics.

From the internal structural evidence, in the form of the modulus of rigidity of the successive internodes along the stem, it was shown that minor changes in value of the modulus could be correlated with the presence of branches at the nodes. The major inflection at the maximum of the distribution in mass, length, volume or slenderness ratio curve was correlated with the major change in the values of the modulus of elasticity. These latter changes were attributed to the inception of the floral axis at the node lying nearest to the maximum of the distribution curves. It was found that branching did not effect the over-all contour of the distribution curve. Instead, branching produced only local changes in the contour of the distribution curves. The appearance of a branch or bud at a node depressed the rate of growth and locally changed the elastic modulus. If the branch appeared at a low node the depression of the rate of growth was more marked than if the branches appeared at an upper node.

The data support the assumption that the completed static structure of a grass, when analyzed in terms of the physical attribute of the internodes as a function of the numerical position of these internodes along the stem, reflected the growth-in-time history of the plant.

Since none of the available data showed the accelerating phase of growth to be representable by a simple logarithmic function, it is suggested that the departure is due to the presence of secondary growths, which distort the expected ideal functional relation.

The modulus of elasticity of *Arundo donax* was found to be about a million pounds per square inch, comparable to that of white cedar. Southern industries are probably not aware of the economic value and strength of this material.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 3, PP. 232–239 MAY, 1947

LEAF ANATOMY OF STREPTOCHAETA AND THE RELATION OF THIS GENUS TO THE BAMBOOS[1]

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In connection with the study of the morphology of *Streptochaeta*, it was pointed out to me that the leaf-blades of *Streptochaeta spicata* contain a special kind of tissue composed of greatly enlarged cells which collapse at maturity. The study of these cells was approached with two objects in mind. In the first place the cells are of interest from the standpoint of development because of their extremely large size and the uniform way in which they collapse. In the second place the presence of similar tissues in bamboos and grasses of uncertain affinities presents an interesting problem in phylogeny. Brandis (1907) has already described the characteristic pattern of bamboo leaves and has shown that leaves of members of the Phareae are very similar. I have been able to add *Streptochaeta*, *Anomochloa*, *Pariana*, *Lithachne*, *Mniochloa*, and *Raddia* to the list. Not only are the enlarged cells present in the leaves of all these grasses, but their leaf anatomy is so strikingly similar that one is forced to consider the possibility of relationship among them.

Living material of *Streptochaeta spicata* Schrad. and *Pharus latifolius* L. was available from plants growing in the Indiana University greenhouse. Through the kindness of Mrs. Chase of the National Herbarium, pieces of leaves were obtained from herbarium specimens of various species of bamboo and of *Pariana zingiberina* Doell, *Leptaspis angustifolia* Summerheyes and C. E. Hubbard. Dr. Smith of the Gray Herbarium has generously provided herbarium material of *Mniochloa strephioides* (Griseb.) Chase, *Raddia brasiliensis* Bertol, *Lithachne pauciflora* (Swartz) Beauv., and several species of bamboo. Fixed material of *Olyra heliconia* Lindm., *Pharus parvifolius* Nash, and *Streptochaeta Sodiroana* Hack. was obtained from the collection of Dr. Weatherwax. Although scarcity of material prohibited my securing a piece of the only leaf of *Anomochloa marantoides* Brongn. in the National Herbarium, it was possible to discern the presence of the large mesophyll cells with the aid of a hand lens. Since most of this study dealt with leaves of *S. spicata*, the bulk of the discussion will be devoted to that species.

The appearance of *Streptochaeta* is very unlike that of grasses native to the temperate zone. Like many tropical grasses it bears leaves whose blades

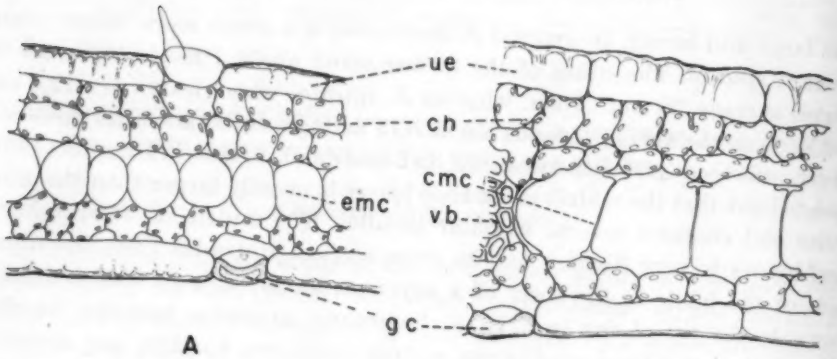
[1] The author gratefully acknowledges the guidance and encouragement of Dr. Paul Weatherwax who suggested the investigation of the collapsed cells. She is also indebted to Dr. Ralph H. Wetmore for reading the manuscript.

are large and broad. In general *S. Sodiroana* is a much more robust plant than *S. spicata*. The culms of the former stand about 1 meter high and its leaves average 25 cm. × 7 cm. whereas *S. spicata*, whose leaves are 12.5 cm. × 4.5 cm. on the average, stands about 0.75 m. high. In both species there is a short, pubescent petiole between the leaf-blade and its sheath. Brandis (1907) pointed out that the midrib of bamboo leaves is usually larger than the other veins and contains several vascular bundles. The midrib of *Streptochaeta* leaf-blades is very distinct and in cross section protrudes from the upper side of the blade in the form of a keystone which becomes less noticeable towards the tip of the leaf. In *S. Sodiroana* numerous vascular bundles occupy the peripheral zone of the midrib, while two bundles, one dorsal to the other, lie in the center. The peripheral bundles are absent in *S. spicata*, although the two (sometimes three) median bundles are present. Although all grass leaves are characterized by parallel longitudinal vascular bundles, the veins in the leaf-blades of most of the generally recognized tribes are connected occasionally by cross veins. In the leaves of most bamboos, *Streptochaeta* and the few genera mentioned above, these cross anastomoses are characteristic.

Transverse sections of the leaf-blade (fig. 1 C) reveal a pattern which emphasizes its resemblance to leaves of bamboo (fig. 3 C). When the leaf is mature, it contains six layers of cells: the upper and lower epidermis, three layers of chlorenchyma, and a special kind of tissue composed of very large cells. The upper epidermis consists of flat, laterally lobed, elongated cells interrupted by occasional stomata and trichomes. Stomata in the lower epidermis are more numerous and are arranged in longitudinal rows on each side of the longitudinal veins immediately above the special large cells. Next to the lower epidermis there is one layer of green cells, and below the upper epidermis there are two layers. These mesophyll cells are irregularly lobed or cleft and are so arranged that they surround numerous intercellular spaces. The upper and lower regions of chlorenchyma are separated by the layer of enlarged cells. These cells are elongated transversely to approximately 4–6 times their height.

A cross section does not present a continuous row of enlarged cells across the leaf, but an alternation of these cells (fig. 1 C, *emc*) with lobed chlorenchyma cells (fig. 1 C, *cch*) and sheathed vascular bundles (fig. 1 C, *p*). There are usually four cells between the vascular bundles; two large cells separated by two chlorenchyma cells, although sometimes there may be only one or as many as three chlorenchyma cells or all the cells between the longitudinal veins may be enlarged. The bulliform cells occur just above the green cells which separate enlarged cells.

A longitudinal section of a leaf of *Streptochaeta* presents a very different picture (fig. 1 B). In *S. spicata* the side walls of the cells, which in cross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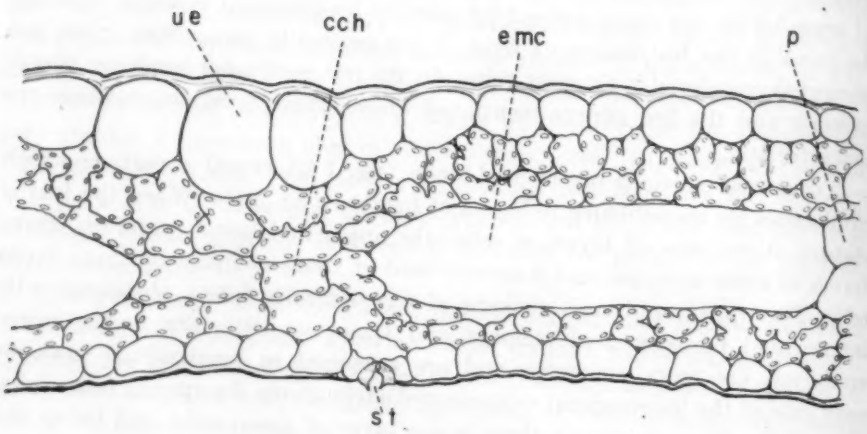
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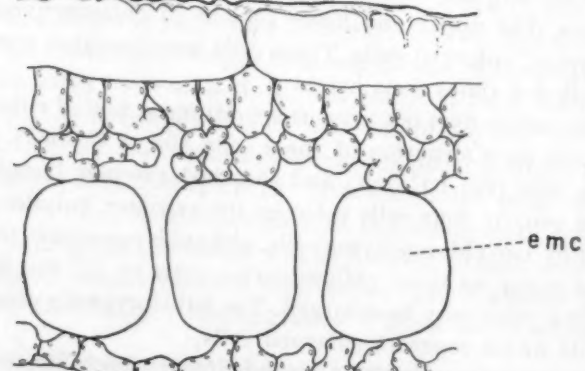
emc
D

section are elongated, are collapsed in such a way that the tissue appears as a row of "I's." Between the collapsed cells there are large spaces which connect with the intercellular spaces of the chlorenchyma and thence to the stomata. The enlarged cells are devoid of chloroplasts and contain only dead cytoplasm. The large cells fail to collapse in *S. Sodiroana*. They die, but instead of caving in, they become very round and separated from one another (fig. 1 D), although they remain attached to the mesophyll above and below, and to the connecting chlorenchyma and the vascular bundles at either end. This same configuration is also found in the leaf-blades of *Pharus latifolius*, except that the large cells do not become separated to the extent that they are in *S. Sodiroana*. Occasionally the cells will collapse, in which case they form the typical I-beam structure. In bamboos which have been examined the large cells collapse as they do in *S. spicata*.

Studies on the ontogeny of the leaf of *S. spicata* reveal that some of the cells which are destined to collapse are determined soon after the leaf-blade is formed and arise in a definite relation to the longitudinal veins. Early in development the blade is composed of five layers of actively dividing cells. Differentiation of the main longitudinal vascular bundles occurs first and the other bundles develop later. When the leaf blade is about half of a millimeter in width (fig. 2 A), only seven or nine bundles of provascular tissue can be discerned in cross section, whereas there are approximately forty bundles in the fully developed leaf. As the secondary veins develop from the middle layer, the cells adjacent to them begin to enlarge vertically at first and then laterally (fig. 2 B). The enlargement of these cells seems to keep pace with the rapid increase in number of cells in the surrounding tissues and consequent increase in dimensions of the growing leaf. Some time during the initial enlargement of the middle layer of cells, cells in the layer immediately above divide horizontally forming the sixth layer (fig. 2 C). Although the rapidly enlarging cells cease to divide in a lateral and vertical plane, they continue to divide in a direction parallel to the longitudinal axis of the leaf at the same rate as the embryonic chlorenchyma cells until cell differentiation begins.

By the time the leaf-blade is about 3.5 mm. wide, all the vascular bundles have been determined, and there are usually four cells in the middle layer between every two bundles so that the pattern is essentially that of the

Explanation of figure 1

Sections of leaf-blades of *Streptochaeta*. A. Longitudinal section of portion of young leaf of *S. spicata* prior to collapsing of enlarged mesophyll cells. B. Longitudinal section of portion of mature leaf of *S. spicata*. C. Transverse section of portion of mature leaf-blade of *S. spicata*. D. Longitudinal section of portion of mature leaf-blade of *S. Sodiroana*. *ch*—chlorenchyma; *cch*—chlorenchyma connecting enlarged cells; *emc*—enlarged mesophyll cell; *gc*—guard cells; *p*—parenchyma sheath of vascular bundles; *st*—stoma; *uc*—upper epidermis; *vb*—vascular bundles.

mature leaf (fig. 2 C). The middle two members (fig. 2 C, *cch*) of this quartet of cells cease enlarging as soon as they reach the dimensions of a mature chlorenchyma cell, while the outer two (fig. 2 C, *em*) continue to grow. The cytoplasm becomes highly vacuolated in the large cells as they increase in size, whereas it remains dense in the cells of the other layers and of the developing vascular bundles until division ceases and differentiation begins.

Up to the time the blade has emerged from the enclosing sheath of the next lower leaf and has begun to unfold, the enlarged cells of the middle layer are rectangular in shape in longitudinal section and their contents are alive. In surface view they are very long and narrow and are closely packed together. Their nuclei fill the entire width of the cell. At this time, longi-

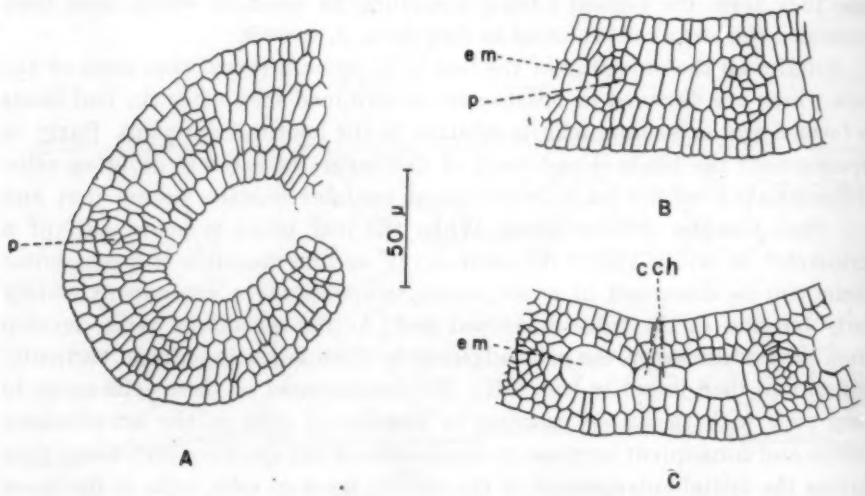

FIG. 2. Transverse sections of young leaves of *S. spicata*. A. Portion of leaf 0.5 mm. broad showing formation of main vascular bundles. B. portion of leaf 2.1 mm. broad showing middle layer of mesophyll beginning to enlarge. C. Portion of leaf 3.5 mm. broad showing adult pattern and formation of sixth layer of cells. *em*—enlarging mesophyll cell; *cch*—chlorenchyma cells connecting two enlarged cells; *p*—procambium.

tudinal sections show small intercellular spaces between enlarged cells where the corners have become rounded and the walls separated. In general the nuclei of these enlarged cells are slightly larger than those of the embryonic chlorenchyma cells, although by the time they have reached their full dimensions, the nuclei of all the mesophyll cells are of approximately the same size.

Just before or soon after unfolding of the leaf-blade, the enlarged cells appear to die, and their walls collapse. The regularity in form of the collapsed cells of the mature leaf seems to indicate that some force was operating on all of them at the same time. The nature of this force has not yet been determined.

The preceding description of the leaf anatomy of *Streptochaeta spicata*

presents a general picture of the bamboo type of leaf pattern. Brandis (1907) in his discussion of bamboo leaves listed several characters which distinguish them from those of other grasses. Among the most important are the following:

1. Full grown leaves flat, with a prominent midrib containing a number of vascular bundles in two lines.

2. Stomata abundant on lower epidermis over chlorophyll parenchyma in longitudinal belts alternating with belts without stomata.

3. Thick-walled lower epidermis with numerous protuberances. Upper epidermis generally smooth.

4. Large apparent cavities in mesophyll between long nerves and bands of bulliform cells, which are filled by flat, thin-walled cells lying upon each other like the leaves of a book. (These are the collapsed enlarged cells). Walls of flat cells collapsing when leaf is full grown leaving large intercellular spaces.

5. Chlorophyll tissue never limited to cylinders around vascular bundles.

6. All chlorophyll cells with peculiar folds in wall dividing each cell into a number of usually incomplete tubes.

It must be emphasized that all these characters are not constant throughout the Bambuseae, nor are all peculiar to the tribe. For instance, in *Chusquea abutifolia* Griseb. there is only one vascular bundle in the midrib. The lower epidermis in *Chusquea sulcata* Swallen is not papillate and the chlorenchyma cells are only slightly cleft. The features which are most constant are the enlarged mesophyll cells, the arrangement of the stomata, the shape of the chlorenchyma cells, the presence of cross veins and in addition, the arrangement of the various tissues. The enlarged cells are usually collapsed, although in some species they remain distended. The deeply cleft chlorenchyma cells are flat in longitudinal sections and are compactly arranged in layers. There are five or six, or sometimes seven, layers of cells in the leaf. Above the enlarged cells there are two or three layers of chlorenchyma and below them one or two layers. Longitudinal bands of collapsed cells alternate laterally with vascular bundles and bands of chlorenchyma one or two cells wide in precisely the same manner as described for *Streptochaeta* (fig. 3 C).

As was mentioned in the beginning, several genera not included in the Bambuseae also possess these same leaf characteristics. These genera (fig. 3) include *Pharus, Leptaspis, Olyra,* and *Diandrolyra* as mentioned by Brandis (1907) and *Lithachne, Mniochloa, Raddia, Pariana,* and possibly *Anomochloa.* All these genera and *Streptochaeta* possess most of the features mentioned by Brandis as being characteristic of bamboo leaves. The large mesophyll cells which may or may not collapse and the spatial arrangement of veins, enlarged cells, and chlorenchyma as described for bamboo and *Streptochaeta* are characteristic of all eight genera. The chlorenchyma is arranged

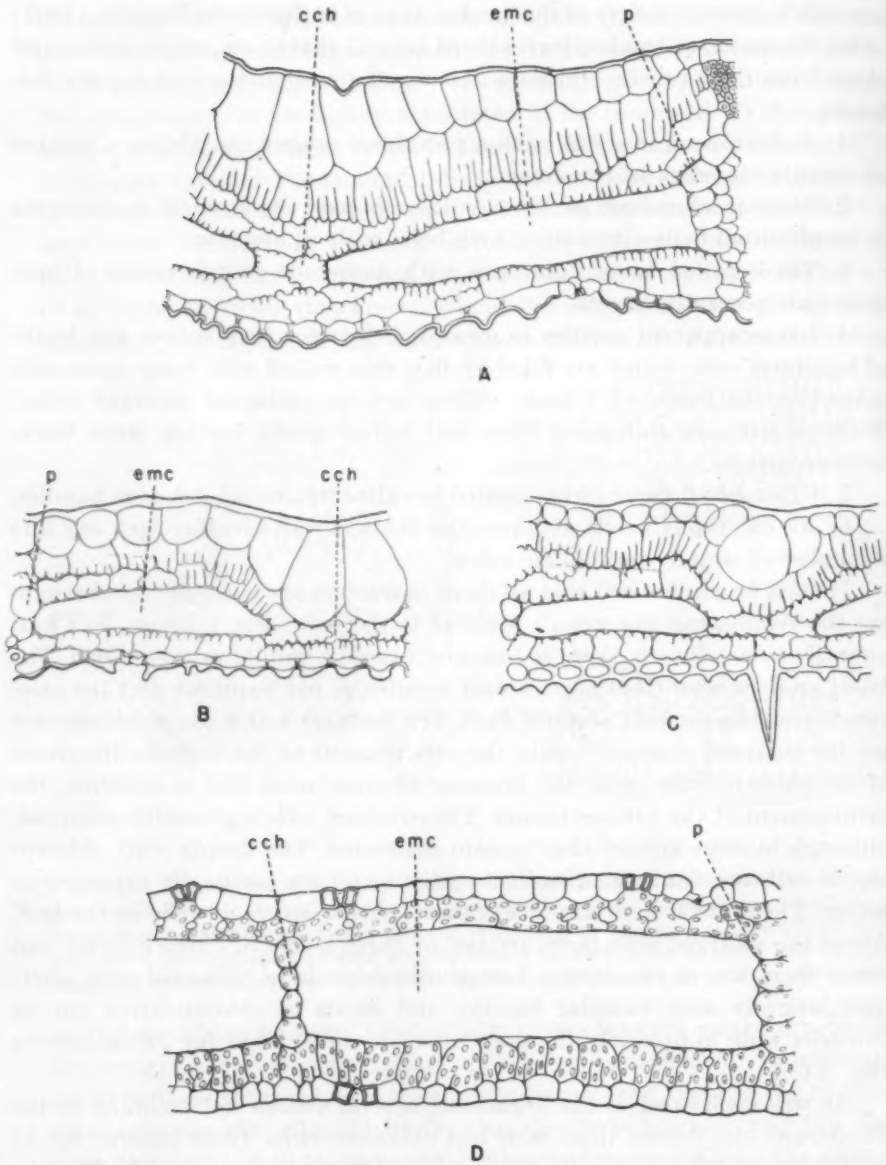

FIG. 3. Transverse sections of portions of leaf blades. A. *Olyra heliconia*. B. *Pariana zingiberina*. C. *Phyllostachys bambusoides* (after Brandis 1907). D. *Pharus parvifolius*. *cch*—chlorenchyma cells connecting enlarged cells; *emc*—enlarged mesophyll cells; p—*parenchyma* sheath of vascular bundles.

in layers above and below the enlarged cells rather than in cylinders around the vascular bundles as it is in many grasses of other tribes. In *Pharus* and *Olyra* the midrib contains two or more vascular bundles. In all the genera the stomata are arranged in longitudinal rows on each side of the vascular bundles and alternate with longitudinal bands of epidermis which are devoid of stomata. The chlorenchyma of *Pharus*, *Leptaspis*, and *Streptochaeta* differs from the typical bamboo type in that the tissue is less compact, the individual cells are not flat, and their lobes are spread out. The enlarged cells in *Pharus* and *Leptaspis* are of very great size, and the chlorenchyma connecting them is a vertical column one cell wide consisting of three or four very small cells (fig. 3 D). In *Pariana* there may be more than three chlorenchyma cells connecting the enlarged cells (fig. 3 B).

In spite of minor differences in leaf structure between these grasses and the bamboos, the basic pattern is so similar that relationship is suggested. All the genera are of doubtful affinities and have been placed in various tribes depending on the interpretation of their spikelets. For example: the floral structure of *Streptochaeta* is such that an interpretation of it has been difficult. As a result there have been several explanations and the genus has been classified in almost as many ways as there are interpretations. Originally it was regarded as a special subtribe of the Bambusaceae by Doell (1880), whose opinion is upheld by Mrs. Arber (1929). Celakovsky (1889) and Goebel (1895) considered it very primitive and very close to the ancestral type of grass. Hackel (1887) assigned it to the Oryzeae, while Bentham and Hooker (1883) placed it in the Paniceae. The leaf anatomy, however, favors the opinion of Doell and Arber, and it will be shown in a later publication that the structure of the inflorescence may bear this out. Further study of the inflorescences of the other genera, keeping in mind the possibility of their affinities with the Bambuseae, may prove fruitful.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 3, PP. 240–249 MAY, 1947

MEGASPOROGENESIS AND EMBRYO DEVELOPMENT IN TROPAEOLUM MAJUS L.[1]

RUTH I. WALKER

The mature eight-nucleate female gametophyte of *Tropaeolum majus* L. was described briefly by Woycicki in 1907 (5). Studies on the development of the embryo had been made much earlier. Wilson in 1843 (4) described a root-like process at the base of the bottle-shaped embryo from which two branches arise; one branch perforates the ovule below the micropyle and passes around the ovule in the carpel cavity; the other grows through the funiculus to the placental vascular bundle and downward to the point of union of the carpel and receptacle. Schacht in 1855 (2) reported the formation of two "limbs" from an embryo body; one penetrating the ovary wall, the other growing through the micropyle and into the stylar canal. Observations similar to those of Wilson were later confirmed by Dickson in 1872 (1). He found also that in *T. peregrinum* L. the first branch of the process grew only a short distance in the ovarian cavity and then penetrated the carpel wall, growing obliquely outward and downward, and that in *T. speciosum* Poepp. & Endl. the placental process did not develop.

MATERIALS AND METHODS

Material from two varieties of cultivated nasturtium, the single, climbing type and the ordinary double Golden Gleam, were used in this investigation. Flower buds of various ages, open flowers, and fruits in various stages of development were collected and fixed in Karpechenko's modification of Nawaschin's and formal-acetic-alcohol solutions. The material was embedded in paraffin and sections 10 to 30 μ in thickness were cut, mounted, and stained with either Heidenhain's iron-alum or Delafield's haematoxylin.

MEGAGAMETOPHYTE DEVELOPMENT

The ovary contains from three to five ovules. Each ovule arises as a rounded mass of cells from the surface of the placental tissue at the base of a carpel, and continues to develop by nuclear and cell division. Growth occurs more rapidly on one side of the protuberance than on the other, with the result that the ovule bends toward the stylar end of the ovary (fig. 1).

The inner integument arises from the ovule at a level immediately below the megaspore mother-cell and grows outward and forward around the

[1] The writer wishes to express her appreciation for support of the work from the Wisconsin Alumni Research Foundation.

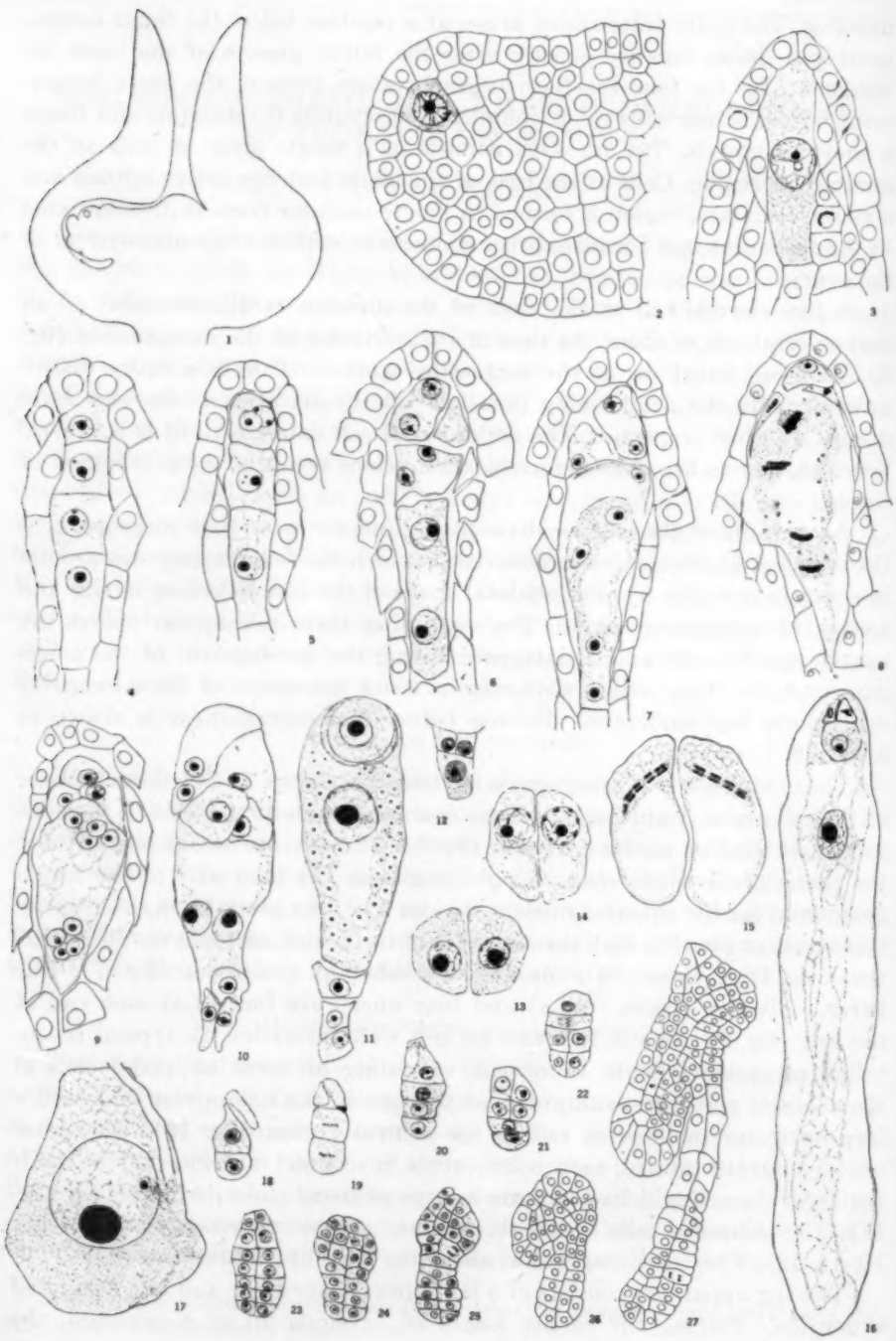
nucellus. The outer integument arises at a position below the inner integument and grows forward shortly after the initial growth of the inner integument. By the time the four megaspores are formed, the inner integument, which is four cells thick, completely surrounds the nucellus and forms a short micropyle. The nucellus persists as a single layer of cells in the micropylar region. Cells at the base of the ovule undergo active mitosis and a massive chalazal region is formed. A single vascular trace is differentiated in the funiculus and forms a direct connection with the vascular system of the ovary.

A hypodermal cell at the apex of the nucellus is differentiated as an archesporial cell at about the time of the initiation of the integuments (fig. 2). This cell functions as the megaspore mother-cell and is easily distinguished from the neighboring nucellar cells by its greater size and more deeply staining properties. The archesporial cell enlarges until it is several times as long as broad at maturity, the nucleus being in the mid-region of the cell (fig. 3).

As a result of the meiotic divisions, a linear row of four megaspores is formed (fig. 4). Ovules were observed in which the four megaspores are not in a linear row (fig. 5). The chalazal spore of the row increases in size and forms the megagametophyte. The remaining three micropylar spores are nearly equal in size and disintegrate during the development of the megagametophyte. Many ovules were seen in which the nuclei of the micropylar megaspores had undergone division before disintegration, as is shown in figures 6, 7, and 10.

The cytoplasm of the megaspore is highly vacuolate. The vacuoles coalesce as the cell grows, resulting in a large central vacuole at the time of the completion of the first nuclear division (fig. 6). The micropylar nucleus divides, the plane of division being at right angles to the long axis of the megagametophyte; the chalazal nucleus divides also, the plane of division being transverse or parallel with the long axis of the megagametophyte. The nuclei resulting from these divisions are embedded in cytoplasm (fig. 7). One further division occurs (fig. 8) and four nuclei are formed at each end of the cell (fig. 9); this is followed by cell wall formation. A typical seven-celled megagametophyte is formed, consisting of three antipodal cells at the chalazal end, two synergids and the egg of the micropylar end, and a large primary endosperm cell in the central region (fig. 10). The polar nuclei migrate toward each other, come in contact anterior to the mid-region of the cell and fuse to form a large primary endosperm nucleus (fig. 11). The antipodal cells are small and may assume varying positions (figs. 10, 11, 12). They distintegrate at about the time of fertilization.

The egg apparatus consists of a large pear-shaped egg and two elongated synergids. During the earlier stages of development of a synergid, the



nucleus is centrally located and surrounded by finely vacuolate cytoplasm (fig. 13). A large vacuole appears at the micropylar end of the cell which later disappears and a new vacuole is formed at the base of the cell (fig. 14). Synergid nuclei appear to be in the process of mitosis although none was observed in which division was completed (fig. 15). The egg cell grows and the large basal portion extends into the megagametophyte beyond the synergids. The egg nucleus is located toward the basal portion of the cell and is embedded in cytoplasm. Starch grains are abundant in the cytoplasm surrounding the egg nucleus and in the young endosperm mother cell but none are present in either the antipodals or the synergids (fig. 11).

FERTILIZATION

Fertilization takes place from 12 to 19 hours after pollination. In this process the pollen tube grows through the micropyle and enters the megagametophyte between the two synergids. The synergids are not destroyed by the entrance of the pollen tube and may persist until the four-celled embryo stage (fig. 20). No early stages of the union of one of the male nuclei with the egg nucleus were observed. Figure 17 shows a young zygote nucleus in which the chromatic network of the male and female nuclei are indistinguishable from one another. Two nucleoli are now visible in the zygote nucleus, the larger, the nucleolus of the female gamete, and the smaller, the nucleolus of the male gamete. The second male nucleus fuses with the endosperm. Division of the endosperm nucleus occurs shortly after fertilization. Often two or four endosperm nuclei are found before the first division of the zygote has occurred.

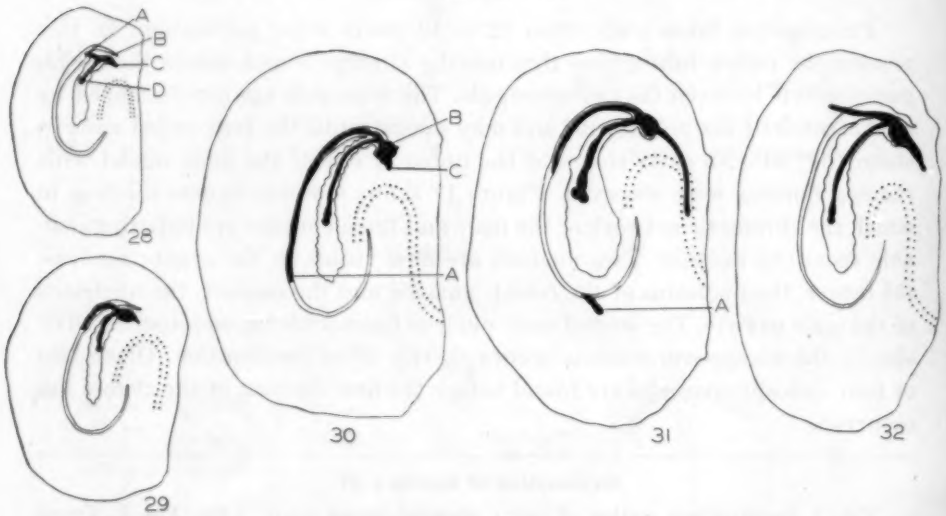
Explanation of figures 1–27

FIG. 1. Longitudinal section of ovary showing young ovule. ×30. FIG. 2. Young ovule with hypodermal archesporial cell. ×375. FIG. 3. Nucellus, megaspore mother-cell. ×375. FIG. 4. Linear row of four megaspores. ×375. FIG. 5. T-shape tetrad of megaspores. ×375. FIGS. 6–15. Stages in the development of the megagametophyte. FIG. 6. Two nucleate megagametophyte and disintegrating megaspores. ×375. FIG. 7. Four nucleate megagametophyte and disintegrating megaspores. ×375. FIG. 8. Third nuclear division. ×375. FIG. 9. Eight-nucleate megagametophyte. ×375. FIG. 10. Young megagametophyte before fusion of the polar nuclei. ×375. FIG. 11. Older megagametophyte, polar nuclei fused. ×375. FIG. 12. Antipodals of megagametophyte. ×375. FIG. 13. Young synergids. ×600. FIG. 14. Older synergids. ×600. FIG. 15. Still older synergids at time of fertilization ×600. FIG. 16. Mature megagametophyte. ×140. FIG 17. Young zygote showing remains of pollen tube. ×600. FIG. 18. Two-celled proembryo, remains of one synergid. ×140. FIG. 19. Two-celled proembryo, nuclei in process of division. ×140. FIG. 20. Four-celled proembryo, remains of one synergid present. ×140. FIG. 21. Vertical division of haustoria cells. ×140. FIG. 22. Vertical division of apical and suspensor cells. ×140. FIG. 23. Further development of embryo, suspensor and haustoria. ×140. FIG. 24. The same. ×140. FIG. 25. The same. ×140. FIG. 26. Initiation of the first haustorium. ×140. FIG. 27. Older embryo, suspensor and haustoria. ×140.

EMBRYO DEVELOPMENT

The zygote divides transversely to form a two-celled proembryo, the two cells approximately equal in size (fig. 18). Both cells divide to produce a linear row of four cells (figs. 19, 20). The embryo develops from the apical cell of the tier, the suspensor is formed from the subapical, and the haustoria develop from the remaining two cells. Further divisions occur in the four cells, the plane of division being first vertical and then horizontal (figs. 21, 22), so that a 14- to 16-celled proembryo is formed (fig. 23).

The basal cells of the proembryo continue to multiply more rapidly than the apical and suspensor cells, forming a wedge-shaped mass (figs. 24, 25, 26, 27). Peripheral cells of this mass adjacent to the suspensor and on the



FIGS. 28–32. ×25. FIG. 28. Longitudinal section of carpel showing outline drawing of embryo, suspensor and haustoria. FIG. 29. The same showing first haustorium in carpel cavity. FIG. 30. The same showing older stage of first haustorium in carpel cavity. FIG. 31. The same showing first haustorium in carpel wall. FIG. 32. The same showing growth of first haustorium in carpel wall.

side opposite the funiculus become actively meristematic and a root-like haustorium is initiated which penetrates the integument near the micropyle and grows around the ovule in the carpel cavity and into the carpel wall (figs. 28, 29, 30, 31). Haustoria were observed penetrating the carpel wall opposite the micropyle (fig. 32). This was reported by Dickson as the characteristic condition for *T. speciosum* and *T. peregrinum*.

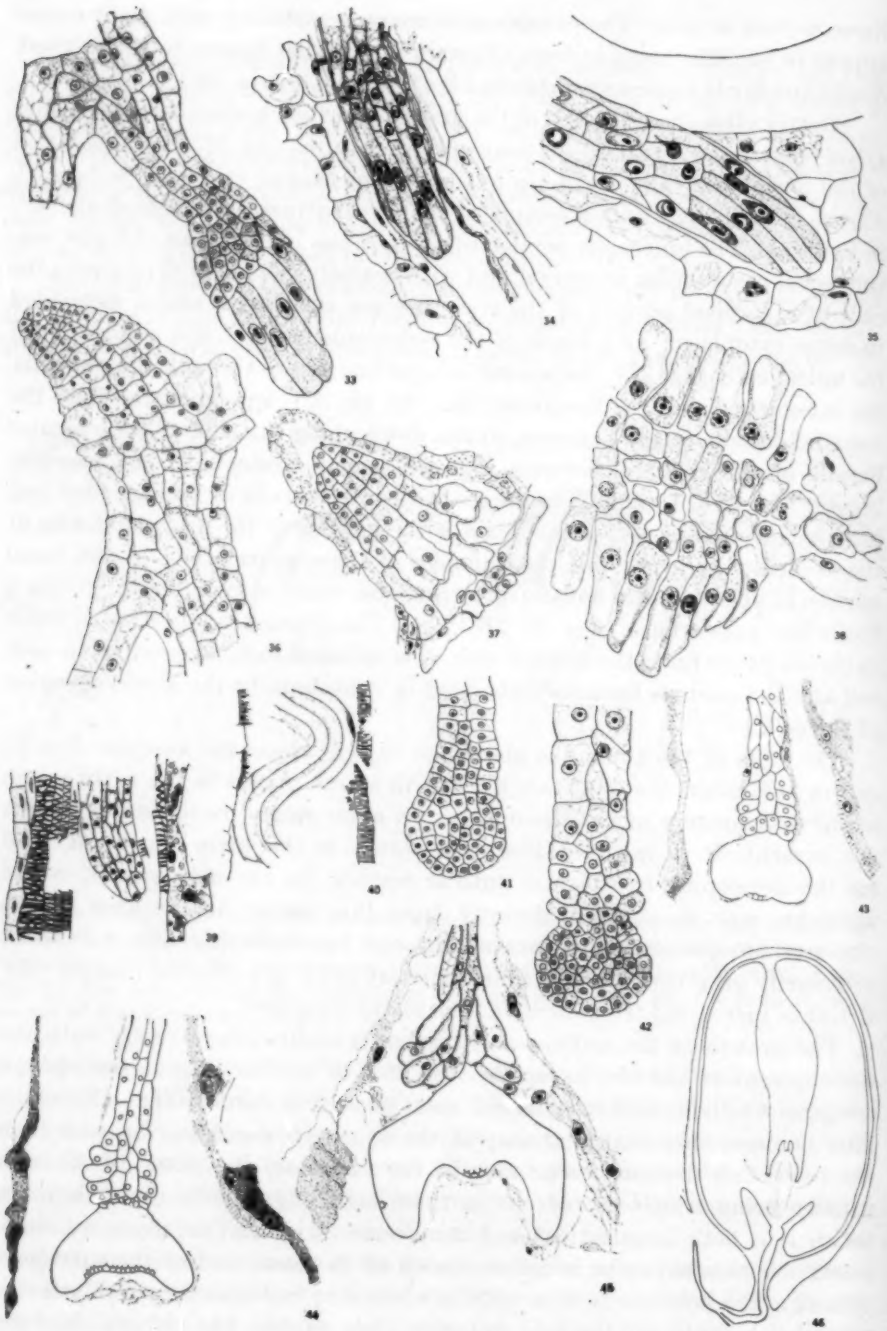
Early in the development of the haustorium, the apical cells of the structure are elongate in shape and contain dense cytoplasm with large nuclei (figs. 33, 34, 35). As growth continues, they become from three to seven

times as long as wide. The cytoplasm is coarsely vacuolate and giant nuclei appear to be undergoing mitosis although no division figures were observed. Nuclei similar to these were described by Woycicki (6) in 1907.

Shortly after the initiation of the first haustorium, a second protuberance arises from the peripheral cells nearest the funiculus (fig. 27). Multiplication of the peripheral cells continues until a wedge-shaped structure is formed. Figure 36 is a longitudinal section of such a structure as indicated at "C" in figure 28. The innermost portion of this process is composed of large, mature cells, rectangular in section and with coarsely vacuolate cytoplasm; the cells at the apical portion of the structure are small with nuclei embedded in dense cytoplasm. As a result of the embryonic activity and elongation of the apical cells (fig. 37), the second haustorium grows through the nucellus, the integument and the funiculus (figs. 28, 29, 30), and upon reaching the vascular bundle of the placenta, grows down along the side of the vascular bundle of the raphe or between the component elements of the vascular bundle (fig. 31). The haustorium pushes aside the cells of the nucellus and integument until it comes in contact with the cells of the vascular tissue of the funiculus. During this development the peripheral cells of the basal portion of the placental haustorium grow also, especially in length, giving a finger-like appearance (figs. 30 "B," 38). This elongation may be as much as three or four times the original size. A large basal vacuole develops in each cell and the nucleus becomes embedded in cytoplasm in the anterior region of the cell.

The cells of the funiculus above the region where the vascular bundle curves and enters the ovule are filled with starch grains in the early stages of the development of the haustorium. In older stages, fewer starch grains are present. It is assumed that this starch is the main source of food for the developing haustorium until it reaches the vascular bundle, where nutrients may be absorbed directly from this tissue. As the apex of the placental haustorium grows forward through the raphe (fig. 39), it does not necessarily grow directly downward but may grow in a curving manner (fig. 40), thus increasing the absorbing area of the structure.

The growth of the embryo and suspensor occurs concurrently with the development of the two haustoria (fig. 28 "D"). The cells of the embryo continue to divide and a spherical mass of cells is formed (fig. 41) which later becomes somewhat pear-shaped, the apical portion being broader than the base. Cell divisons occur also in the supensor, the plane of division usually being transverse except in those cells adjacent to the embryo in which it is both longitudinal and transverse. A collar-like structure, composed of elongated cells, is differentiated at the basal end of the suspensor (fig. 42). The position of these cells in relation to endosperm probably facilitates the absorption of the food materials (figs. 44, 45). The elongation of the suspensor pushes the embryo into the endosperm.



The cotyledons appear as two lateral outgrowths at the apex of the embryo opposite each other (fig. 43). The epicotyl develops as a small outgrowth between the cotyledons at the apex of the embryo. Basal cells of the embryo later form the hypocotyl (figs. 44, 45) The cotyledons elongate rapidly, forming two larger fleshy structures at maturity. A mature embryo showing the differentiation of vascular strands is shown in figure 46.

The growth of the embryo is accompanied by increase in size of the growing seed. The cells of the integuments and of the nucellus adjacent to the chalazal region multiply rapidly; the plane of division of the integumentary cells is such that it does not increase materially in thickness. The nucellus, which is wide at the base and tapers toward the micropylar end of the ovule, consists of an outer layer of small, densely staining cells and an inner layer of large, irregularly shaped cells, with central vacules and little cytoplasm. These become disorganized and are absorbed by the endosperm.

The development of the embryo and surrounding tissue is dependent upon the nutrient materials brought into the ovule by the vascular tissue from the adjacent parts of the plant. In the early stages of growth some of the nutrients are stored as starch in the cells of the funiculus just above the entrance of the vascular bundle into the ovule. The greatest amount of starch is observed in these cells when the embryo is about five days old. As the embryo and haustoria mature, the food is digested and absorbed by the peripheral cells. During this time the endosperm develops slowly; some of the nuclei are found in a thin layer of cytoplasm adjacent to the embryo, while others are embedded in dense cytoplasm contiguous to the nucellus (fig. 43). The endosperm remains free-nucleate throughout its entire development. No trace of the endosperm or nucellus is found at maturity and the seed consists of the embryo surrounded by the seed coat through which extends the slender, thread-like haustorium.

Explanation of figures 33–46

FIG. 33. Detailed drawing of apical portion of young haustorium indicated at "A" in figure 28. × 140. FIG. 34. The same for older haustorium in carpel cavity as indicated at "A" in figure 30. × 90. FIG. 35. The same for older haustorium in carpel wall as indicated at "A" in figure 31. × 90. FIG. 36. Detailed drawing of placental haustorium as indicated at "C" in figure 28. × 140. FIG. 37. The same for apical portion of an older placental haustorium indicated at "C" in figure 30. × 140. FIG. 38. The same for the basal portion of older placental haustorium as indicated at "B" in figure 30. × 140. FIG. 39. Portion of mature placental haustorium adjacent to vascular tissue. × 90. FIG. 40. Curving growth of placental haustorium. × 90. FIG. 41. Detailed drawing of embryo and portion of suspensor as indicated at "D" in figure 28. × 140. FIG. 42. Detailed drawing of somewhat older embryo and portion of suspensor. × 140. FIG. 43. Embryo showing initiation of cotyledons and epicotyl and their relation to the endosperm. × 50. FIG. 44. Somewhat later stage showing embryo and endosperm. × 50. FIG. 45. Still later stage of embryo and endosperm. × 50. FIG. 46. Longitudinal section through maturing ovule showing embryo, suspensor and integuments. × 90.

Abortive ovules commonly occur in *Tropaeolum*, especially in the semi-double Golden Gleam variety. Longitudinal sections of ovaries show that all the ovules of the ovary mature about the same time. Four days after pollination many of the young seeds possess well developed embryos; in others, syngamy has not occurred and the megagametophytes show signs of disintegration. The megagametophytes are much elongated; the egg and primary endosperm nuclei are highly vacuolate and the cytoplasm of the primary endosperm cell has almost disappeared. Nucellar cells are likewise in a state of disorganization. The walls of the cells adjacent to the megagametophyte are thick and have a callus-like appearance. With the increase in age of the ovary, the abortive ovule may enlarge for a time but much less rapidly than the fertilized ovule. Growth finally ceases and the ovule collapses and becomes shrivelled in appearance.

SUMMARY

A single hypodermal cell is differentiated as an archesporial cell in *Tropaeolum majus*. This functions directly as the megaspore mother-cell.

A linear row of four megaspores is formed. Occasionally megaspores may be in a T-shaped arrangement.

The chalazal spore develops into an eight-nucleate, seven-celled megagametophyte; the other megaspores disintegrate.

Syngamy occurs 12–19 hours after pollination.

The synergids are not destroyed as a result of the entrance of the pollen tube and may persist for several days, then disintegrate.

The antipodals disappear before syngamy.

The zygote by transverse divisions forms a row of four cells. The embryo develops from the apical cell of the row, the suspensor from the subapical cell, and the haustoria from the two remaining micropylar cells.

The haustorium which develops first penetrates the integuments below the micropyle and grows around the ovule in the carpel cavity and into the carpel wall opposite the chalazal region of the ovule. The placental haustorium arises later, and grows through the integument and placenta to the point of entry of the vascular bundle of the raphe. The haustoria supply food to the developing embryo.

The endosperm is free-nucleate and is absorbed by the embryo during the course of its development.

The embryo develops in a typical manner having the lateral cotyledons, a terminal epicotyl, and a hypocotyl.

Some ovules may abort through the failure of syngamy.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 3, pp. 250–254 MAY, 1947

HIPPEASTRUM SOLANDRIFLORUM: ITS CHROMOSOMES

J. T. BALDWIN, JR. AND BERNICE M. SPEESE

Hippeastrum solandriflorum (Lindl.) Herb. is found from Brazil to Colombia and the Guianas (Macbride 1936) and, according to the interpretation of Herbert (1837), occurs in several varieties. It was introduced into cultivation in 1820 (Baker 1888) and has been used to a considerable extent in wide crosses, as have many representatives of the genus. Indeed, Bailey (1938) states: "Most of the hippeastrums in cultivation are probably hybrids."

E. P. Killip identified *Baldwin 3099*, now in the U. S. National Herbarium, as *H. solandriflorum*: in flower, September 26, 1943, Braco, Rio Arinos, Matto Grosso, Brazil. The specimen rather well matches *plate 3771* in *Curtis's botanical magazine* for 1840; that illustration is based on a collection made by Schomburgk in British Guiana. In May, 1946, a bulb from the Rio Arinos produced a flowering plant (fig. 1) under greenhouse conditions in Virginia, and, after the scape had withered away, gave rise in September, 1946, to a pair of narrow leaves edged with red. The mature capsule was reddish. Seedlings were grown from that plant.

The senior author found *H. solandriflorum* at three places in Matto Grosso: at Braco, in a sandy area near the Rio Arinos and where grasses, sedges, and trees (among others *Hancornia speciosa* Gomes) are scattered; shortly downstream from Salto Bello on the Rio Sacre; and near Rosario Oéste, across the southern rim of the Amazon Basin, in sandy soil that becomes closely packed when dry and where *Arachis* sp. grows.[1] The hippeastrum was in blossom in September and October, 1943. The flowers were extremely showy. No leaves were present. Populations were large. In two years (1942–1944) of almost continuous travel throughout the Amazonian

[1] It is worthy of record that in September and October, 1943, *Arachis* was observed in flower on the outskirts of Rosario Oéste and also where the road leading northward from that town crosses the rim of the Amazon Basin. The plants of that rim seem in great measure different from those constituting the flora of the regions to the north and south of the rim. On December 3, 1943, in Matto Grosso, flowering specimens were obtained for *A. marginata* Gardn. at Tres Lagóas (*Baldwin 3139*), for *A. Diogoi* Hoehne at Campo Grande (*Baldwin 3140*), for *A. marginata* Gardn. at Corumbá (*Baldwin 3141*): identifications were made by F. C. Hoehne and E. P. Killip. The two collections designated *A. marginata* are of at least varietal difference. The specimens are in the U. S. National Herbarium. The subterranean fruit of *Arachis*, like the pronounced underground development of *Macrosiphonia longiflora* (Desf.) Muell. Arg., of *Anacardium pumilum* St. Hil., and of many other plants of that region, is apparently an adaptation to dryness. Fire may well have served as an agent of selection.

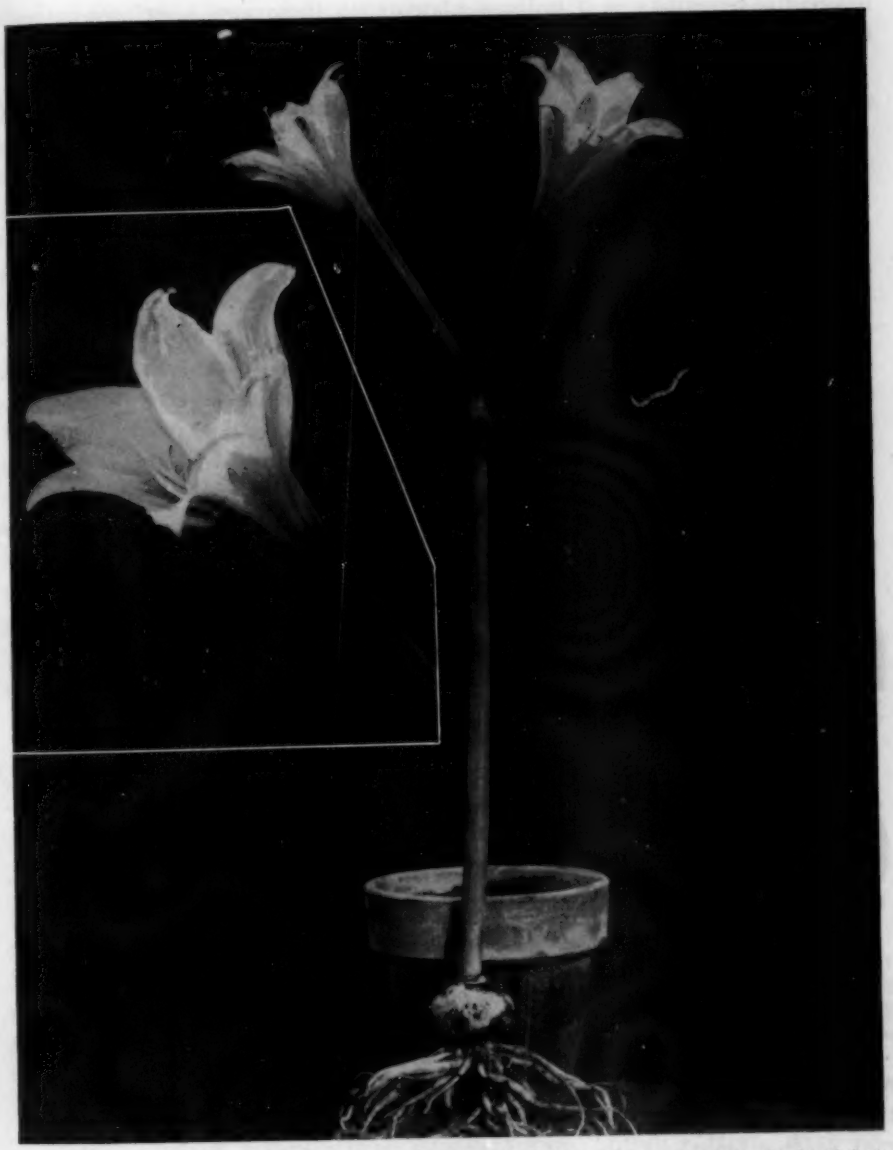

FIG. 1. *Hippeastrum solandriflorum* (Lindl.) Herb.; inset photographed slightly under natural size and reduced about $\frac{1}{3}$ in reproduction.

region and in some of the country immediately south of the Basin, no more impressive assemblages of bulbous plants than these were seen, unless, perhaps, the stands of *Zephyranthes* along the Rio Cuyabá be excepted.

The perianth of *H. solandriflorum* is greenish yellow and reaches a length of eight inches. Two or four flowers are borne on a scape, which may attain

FIGS. 2–4. Chromosomes of *Hippeastrum solandriflorum*, ×1100. FIG. 2. Metaphase from root of Rio Arinos plant with chromosomes distributed in drawing: $2n = 22$. FIGS. 3, 4. Alignment of metaphase chromosomes of two seedlings of Rio Arinos plant. Figure 3 has unequal pair of chromosomes present, as in parent. Figure 4 has no unequal pair of chromosomes.

a height of two and a half feet. The flowers are at first erect but with maturity turn downward. The spathe soon wilts. Leaves are produced later and may reach a length of one and a half feet (Baker 1888) : those of our plant are in November, 1946, not yet six inches long.

Because the Rio Arinos collection had not been "contaminated" through cultivation, it was decided to investigate the chromosomes of that plant and of some of the seedlings raised from it. Preparations were made by the junior

author. Roots were treated with colchicine, fixed in Carnoy's solution (3 absolute alcohol : 1 chloroform : 1 glacial acetic acid), and smeared in propiocarmine.

H. solandriflorum from the Rio Arinos has a $2n$-number of 22 (fig. 2). The plant investigated has one unequal pair of chromosomes. Five of the seedlings grown from that plant have been cytologically studied. Four of them are like the parent, with three pairs of chromosomes in the A group (which has a short short arm), four pairs in the B group (with a longer short arm), three pairs of approximately isobrachial chromosomes in the C group, and an odd pair with one chromosome of the B type and one of the C (fig. 3). Classification into groups is arbitrary but convenient. Obviously, chromosomes in different roots and at different mitotic stages exhibit varying degrees of contraction when treated with colchicine. The fifth seedling has no odd pair of chromosomes (fig. 4) : three pairs are in group A, four in group B, four in group C. If additional seedlings were studied, individuals with five pairs of B-type chromosomes would probably be encountered. Similarly : if the cytological structure of the Rio Arinos population of *H. solandriflorum* were to be analyzed with respect to the classification of chromosomes given here, it would be expected that a great—but unpredictable—percentage of the individuals would have a pair of chromosomes made up of B and C members.

Not many reports of chromosome numbers for *Hippeastrum* have been made:

	$2n$	
H. rutilum	44	Satô (1938)
H. rutilum fulgidum	24(?)	Heitz (1926)
H. vittatum Herb.	46	Nagao & Takusagawa (1932)
"	44	Inariyama (1937)
"	44	Satô (1938)
H. hybridum	44	Inariyama (1937)

Inariyama (1937) and Satô (1938) suggested that their plants were tetraploid; the latter author classified the chromosomes as to types. *H. solandriflorum* from the Rio Arinos is accordingly diploid. A program of hybridization based upon a cytological knowledge of the various species of *Hippeastrum* should be most productive both of scientific and of horticultural results.

SUMMARY

Populations of *Hippeastrum solandriflorum* (Lindl.) Herb. were observed at three places in Matto Grosso, Brazil. A single plant from the Rio Arinos was cytologically studied. It is diploid with a $2n$-number of 22 chromosomes, which can, on the basis of centromere location, be arbitrarily grouped into classes A, B, and C; one chromosome pair, with B and C members, is unequal.

Four of the seedlings grown from the wild plant and investigated were found to be like the parent in having a heteromorphic pair of chromosomes. The fifth seedling examined has no unequal pair of chromosomes: a C chromosome has been substituted for the odd B. If additional seedlings were to be studied, it is likely that individuals with a B chromosome replacing the odd C would be discovered. Accordingly, a considerable number of the plants in the Rio Arinos population should have an unequal pair of chromosomes made up of B and C members.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 3, PP. 255–256 MAY, 1947

ALASKA AND YUKON SPECIES OF RUBUS SUBGENUS CYLACTIS FOCKE

J. P. ANDERSON

In studying the genus *Rubus* for the purpose of writing the manuscript for the Flora of Alaska and adjacent parts of Canada the writer became aware of the differences in treatment of certain groups within the genus by our very best authorities. This is especially true of the species closely related to *R. arcticus* L. Dr. L. H. Bailey,[1] the leading American authority on the genus, believes that the true *R. arcticus* does not occur in North America and includes all American forms of this type in *R. acaulis* Michx. Dr. Eric Hultén[2] of Sweden, the world's leading authority on arctic and boreal plants in general, includes most of the collections in *R. arcticus* but also recognizes *R. acaulis* and hybrids between the two. Bailey describes a new species, *R. alaskensis*, which Hultén regards as a hybrid between *R. arcticus* and *R. stellatus* Smith. After a study of more than three score sheets in my collections, mostly from Alaska but some from Yukon and other parts of northern Canada, I have come to the following conclusions.

RUBUS ARCTICUS L. does occur in North America and *R. acaulis* Michx. should be regarded as a synonym or at best only a forma or subspecies of it. Many intermediate forms occur. If *R. acaulis* is regarded as a separate entity these intermediate forms may be regarded as hybrids, but it seems doubtful if the differences between the two types are sufficient to warrant the separation. Many other species of plants show a similar wide variation.

RUBUS ALASKENSIS is a good species. When Dr. Bailey described this species he had before him three of my collections. No. 2A128 collected on a muskeag 11 miles northwest of Juneau, no. 955 collected at Matanuska, and no. 1378 collected in the valley of the Little Susitna River a short distance above where its canyon emerges from the foothills of the Talkeetna Mountains onto the level stretches of the Susitna-Matanuska valley. Since then I have made additional collections, no. 6981 at the type locality, no. 6989 several miles up the same valley, no. 7208 at Curry, no. 7606 at Talkeetna. It is most common at Talkeetna. Hultén accounts for the large size of this form by hybrid vigor. I do not think that this is at all probable. *Rubus stellatus* is common in the Pacific coastal areas of Alaska but of very scattered occurrence in the interior. *R. arcticus* is common in the interior but reaches

[1] The Genus *Rubus* in North America. Gent. Herb. 5: 24–30, 34–38, 40.

[2] Flora of Alaska and Yukon. Lunds Univ. Årsrk. NF. Avd. 2. 42[1]: 992–997, 1005–1007.

the Pacific coast only at the head of deeply penetrating inlets. Occasional crosses of *R. arcticus* and *stellatus* are found that show no noticeable increase in vigor. It therefore seems unreasonable to assume that hybrids of these two species which are usually less than 20 cm. and often less than 10 cm. tall, and both wholly herbaceous, should in a few instances give rise to a form usually woody at the base and up to 52 cm. tall. When I collected the type number I was so impressed with the size, vigor, and some of the other characteristics of the plants that I thought it might be a cross of the large species with perennial canes, *Rubus spectabilis* Pursh, which was growing near by, and *R. stellatus*. The distribution of *R. alaskensis* is also unfavorable to the hybrid hypothesis. All the specimens except 2A128 were collected in a strip along or near the Alaska Railroad less than 100 miles long in south central Alaska. No *R. arcticus* is known within 50 miles of the place where 2A128 was collected. The leaves and general appearance of *R. alaskensis* are distinctive as compared to its assumed parents. In my opinion no. 955 cited by Bailey is *R. alaskensis* × *arcticus*. All the other numbers cited are typical *Rubus alaskensis*.

Regarding the other two species of the subgenus *Cylactis* in Alaska and Yukon there is no controversy. I collected *Rubus pubescens* Raf. at Watson Lake in Yukon territory but it is not known to reach Alaska. *Rubus pedatus* Smith is common in the Pacific coast regions of Alaska. The five species of the subgenus occurring in Alaska and Yukon may be keyed as follows.

1A. Flowers pink or red.
  1B. Leaves 3-lobed. *R. stellatus.*
  2B. Leaves trifoliate.
    1C. Stems 3–25 cm. tall, entirely herbaceous and slender. *R. arcticus.*
    2C. Stems 20–50 cm. tall, stout and often woody. *R. alaskensis.*
2A. Flowers white.
  1D. Stems slender and creeping, rooting at the nodes, leaves appearing 5-foliate. *R. pedatus.*
  2D. Producing runners but flowering stem arising from the crown, leaves 3-foliate. *R. pubescens.*

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 3, PP. 257–261 MAY, 1947

PLANTS OF IMPORTANCE IN THE BREEDING OF ANOPHELES ALBIMANUS WIED. IN PANAMA[1]

SAMUEL LEWIS MEYER

In Panama, as elsewhere in the Caribbean region, the most important vector of malaria is *Anopheles albimanus* Wied., a "white-footed" mosquito of the group Nyssorhynchus. It is a medium-sized, grayish mosquito which is common in the lowlands of the Caribbean region. Its distribution ranges from Sinaloa, Mexico, to Guayaquil, Ecuador; along the Gulf coast from the lower Rio Grande Valley, Texas, south and east to Surinam; and in the West Indies, except Martinique, St. Lucia, Grenada, and Trinidad (Ross & Roberts 1943). The adult is a strong flier and bites man freely.

Anopheles albimanus breeds in a variety of habitats, including fresh to brackish water, but more abundantly in full sunlight in bodies of water where there are floating mats of vegetation. Within the vegetation mats, the larvae are protected from such natural enemies as surface-feeding fish of various kinds and, at the same time, find an abundant supply of food (Rozeboom 1941). Gatún Lake, the Gatún River, and the Chagres River contain extensive "floating islands" of vegetation which serve as breeding grounds for *Anopheles albimanus*.

In 1944–45, the writer served with the Army School of Malariology in the Canal Zone. At that time, the opportunity was presented to observe the composition of the vegetation mats in the Gatún River and the Chagres River, and the relative importance of the various aquatic plants composing the mats in the breeding of *Anopheles albimanus*. The results of those observations are reported here. The nomenclature used with reference to mosquitoes follows Komp (1942).

It is a well known fact that *Anopheles albimanus* breeds in various types of floating aquatic vegetation in the Canal Zone. Curry (1934) pointed out that *Eichhornia crassipes* (Mart.) Solms, *E. azurea* (Swartz) Kunth, and *Pistia stratiotes* L. were present in abundance in Gatún Lake but stated that the aquatic plants of greatest importance in anopheline breeding were *Utricularia mixta* Barnh. and several species of *Chara* L. The latter plants were said to provide optimum conditions for the breeding of anopheline mosquitoes that require sunlit waters. This was especially true of mosquitoes of the Nyssorhynchus group to which *Anopheles albimanus* belongs.

[1] Contributions from the Botanical Laboratory, The University of Tennessee, N. Ser. No. 95.

The observations of Curry (1934) with reference to *Utricularia* and *Chara* are of particular interest. Matheson (1930) had suggested that *Utricularia* deserved more consideration as a possible agent in mosquito control since larvae were captured in the bladders. Curry, however, pointed out that the surface-feeding and floating habits of anopheline larvae would render them very little susceptible to capture by the submerged traps of *Utricularia*. Matheson also reviewed the conflicting literature with reference to the influence of *Chara* on the development of mosquito larvae. Some workers had indicated a marked inhibitory effect; others observed that the Characeae had little, if any, influence on mosquito breeding. Experimental results of Matheson and Hinman (1929) indicated that certain vigorously growing species of *Chara* in some way prevented the development of larvae, while Matheson (1930) observed that oviposition did not take place where the growth of *Chara* was vigorous. Curry (1934) stated that in tropical and subtropical regions the Characeae favored the development of mosquitoes and that the aquatic flora of *Chara* and *Utricularia* in Gatún Lake provided a breeding place for vast numbers of anophelines. More recently, Rozeboom (1941) reported the Characeae, *Utricularia*, and *Najas* to be especially favorable for the development of *Anopheles albimanus*.

The great vegetation mats in the Chagres and the Gatún Rivers are composed of a relatively small number of species of vascular plants.

Eichhornia crassipes (Mart.) Solms, the common water-hyacinth of South America which has become naturalized in Panama as in some parts of the United States, and *E. azureus* (Swartz) Kunth, the native water-hyacinth of Central America, are found in great abundance. Barber and Hayne (1925) have found anopheline breeding among *E. crassipes* in the southern United States while Eyles and Robertson (1944) reported the same species to be associated with *Anopheles quadrimaculatus* Say in the southeastern United States.

Pistia stratiotes L., the water lettuce, is also present in the vegetation mats. It is widely distributed in tropical regions and seems to be extremely favorable to insect life (Dunn 1934). Though undoubtedly much more intimately associated with the breeding of *Anopheles triannulatus* Neiva & Pinto (Curry 1932; Komp 1942), larvae of *Anopheles albimanus* have been collected from the crowns of *Pistia stratiotes* in the Canal Zone (Zetek 1920). It should be noted that *Anopheles triannulatus*, formerly known as *A. bachmanni* Petrocchi, is of no importance as a vector of malaria in Panama. In Brazil, Bachmann (1921) found that mosquitoes appeared to avoid *Pistia stratiotes*.

Cabomba aquatica Aubl., listed by Standley (1928) as the only Central American species of fanwort, is sometimes found in the mats.

Jussiaea natans H.B.K. is a common floating plant of the Chagres River

and Gatún Lake. It is sometimes found in the vegetation mats. In Panama, larvae of *Anopheles triannulatus* are found along the floating stems (Komp 1942). In the southeastern United States, *Anopheles quadrimaculatus* has been found in association with *Jussiaea diffusa* Forsk. and *J. grandiflora* Michx. (Eyles & Robertson 1944).

The water ferns, *Azolla* Lam., possibly more than one species, and *Salvinia natans* L., are often present, sometimes in sufficient quantity to cover considerable areas. Matheson (1930) called attention to the conflicting observations made on the influence of various species of *Azolla* on mosquito breeding. Some investigators have found species of *Azolla* to be effective

FIG. 1. A view of the Gatún River showing a "floating island" of vegetation, composed principally of *Najas* L.

in preventing anopheline breeding while others have observed a favorable influence.

The most important component of the vegetation mats in the Chagres and Gatún Rivers is *Najas*. It is present in such quantity as to cover extensive areas of water surface (fig. 1). One collection from Gatún Lake and another from the Chagres River have been identified by Clausen (1946) as *Najas arguta* H.B.K., a South American species. The collection from the Chagres River was made by Lt. Harold Trapido, of the Gorgas Memorial Laboratory. Clausen states that "according to Lt. Trapido *N. arguta* is a dominant feature of the aquatic flora of the Chagres River and Gatún Lake, also it is the principal breeding place of *Anopheles albimanus*." Whether the *Najas* in the Gatún River is the same species and whether more than

one species is present in Gatún Lake, the Gatún River, and the Chagres River is not yet known. There is no doubt but that at the present time the most important plant in the Canal Zone from the standpoint of its relation to the breeding of the malaria vector is *Najas*. The "floating islands" of that plant provide a breeding place for incalculable thousands of anopheline mosquitoes.

No mention has been made of *Utricularia* or members of the Characeae. The writer had no opportunity to study the vegetation of Gatún Lake. It is not known whether the Utricularíaceae and Characeae were ever present in such quantity as to be of significance in anopheline breeding in the Chagres and the Gatún Rivers. If that were ever the case, they have now almost completely disappeared and in those areas would certainly no longer be a factor.

It is important to note that Curry (1934) does not mention *Najas* as an important component of the vegetation mats in Gatún Lake. Clausen (1946) cites Lt. Trapido who terms *Najas arguta* H.B.K. the "dominant feature of the aquatic flora" of that part of the Panama Canal system. This indicates that great changes in the composition of the flora of Gatún Lake and, possibly also, the Gatún and Chagres Rivers may have taken place. It is of interest to note in that connection that Curry called attention to the fact that water lettuce had flourished in Gatún Lake for several years and then had "spontaneously and for some unknown reason" almost disappeared.

A factor in producing changes in the observable vegetation pattern of Gatún Lake may have been the erection of Madden Dam across the upper Chagres, a possibility which was recognized and suggested by Curry at the time of its construction. The dam has provided less fluctuation in the water level of the lake and thus there may be less *Chara* and *Utricularia* exposed. At the same time, the reduction in the fluctuation of the water level has apparently provided excellent conditions for the growth of *Najas*.

These observations on the composition of the vegetation mats of two of the rivers of Panama illustrate not only the important role which aquatic vegetation may play in mosquito breeding but also show how the botanist may serve with the entomologist, the parasitologist, and the engineer in attacking the malaria problem.

SUMMARY

The most important vector of malaria in Panama, as in the entire Caribbean region, is *Anopheles albimanus* Wied. It breeds in a variety of habitats, including fresh to brackish water, but most abundantly in full sunlight in bodies of water where there are mats of floating vegetation. The most important elements in the composition of the vegetation mats in the Gatún and Chagres Rivers are: *Najas* sp., possibly *N. arguta* H.B.K., *Eichhornia*

crassipes (Mart.) Solms, *E. azureus* (Swartz) Kunth, *Cabomba aquatica* Aubl., *Jussiaea natans* H.B.K., *Salvinia natans* L., *Azolla* sp., and *Pistia stratiotes* L. Of these, the most important is *Najas*.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 3, PP. 262–266 MAY, 1947

TORREYA

SHORT ARTICLE

Noteworthy Records from the Local Area. During the past few years some very noteworthy botanizing has been carried on by two young botanists in the local area. It has been my privilege to examine most of these collections, and numerous records worthy of publication have come to light. Mr. Harry Ahles has collected over 1175 botanical specimens in Pelham Bay Park in Bronx County, New York, and in some areas of Westchester County. Mr. Joseph V. Monachino has continued collecting in various parts of New York and New Jersey. The following are a few of the most interesting plants found by these collectors, and a corrected identification of one of my own numbers.

Agastache scrophulariaefolia (Willd.) Kuntze—several colonies on a hillside facing east, Van Cortlandt Park, Bronx Co., N. Y., August 12, 1945, *J. V. Monachino 433*. Norman Taylor's "Flora of the Vicinity of New York" says that this species occurs "on the north shore of Long Island and formerly on Staten Island, thence increasing, but never common, northward." This is the first Bronx County specimen in the Local Herbarium at the New York Botanical Garden.

Centaurea vochinensis Bernh.—in a waste lot, North Plainfield, Somerset Co., N. J., August 18, 1934, *H. N. Moldenke 8226*. This collection was originally distributed by me as *C. nigra* L., but Mr. Monachino has kindly pointed out the differences between these two very similar species. *C. nigra* also grows in our local area and is far more common. Gray's "Manual" (ed. 7) states that *C. vochinensis* is found locally from New England to Ontario. Britton & Brown's "Illustrated Flora" (ed. 2) gives its distribution as "Ontario to Massachusetts and southern New York," and Taylor says that it is "rare" from Ontario to southern New York. The New Jersey record therefore appears to be well worth recording.

Cynanchum nigrum (L.) Pers.—along roadsides, section 13, Pelham Bay Park, Bronx Co., N. Y., May 24, 1946, *H. Ahles 276*. The distribution of this European species is given by Gray as from Massachusetts and Vermont to Pennsylvania and Ohio, while Britton & Brown say "Massachusetts to Pennsylvania and Ohio and in British Columbia"; Taylor says "Mass. to Pa. and Ohio."

Elaeagnus umbellata Thunb.—abundantly naturalized in thickets, section 28, Pelham Bay Park, Bronx Co., N. Y., July 11, 1946, *H. Ahles 537*. This Asiatic species is not listed by Gray, Taylor, or Britton & Brown, but is widely naturalized now in our area. I have previously recorded it from various parts of New Jersey.

Euonymus europaeus L.—a single colony found on a rock ledge, in partial shade, section 8, Pelham Bay Park, Bronx Co., N. Y., May 31, 1946, *H. Ahles 305*. Gray says that this European plant "occasionally escapes from cultivation in the Atlantic States," and Taylor says it is "rather rare." The present record seems worth noting.

Lychnis alba var. *colorata* Lange—found along roadsides, section 2, Pelham Bay Park, Bronx Co., N. Y., June 7, 1946, *H. Ahles 376*. This pink-colored form of the

species is not identified in any of our current manuals, although it is listed in most European floras.

Persicaria longiseta (De Bruyn) Moldenke—common on farmland and along roadsides, near Carmel, Cumberland Co., N. J., August 25, 1946, *J. V. Monachino 460*. This east Asiatic ladysthumb, easily the handsomest *en masse* in our area, is not listed in any current manual, but (as was pointed out by me in TORREYA **41**: 201–203) is spreading rapidly along the eastern seaboard.

Plantago Rugelii var. *asperula* Farwell—along shore, section 19, Pelham Bay Park, Bronx Co., N. Y., July 11, 1946, *H. Ahles 549*. Deam's "Flora of Indiana" is practically the only one of our current manuals to list this hairy variety of Rugel's plantain.

Rosa setigera Michx.—along the bridle path, in a naturalized state, Pelham Bay Park, Bronx Co., N. Y., July 19, 1946, *H. Ahles 638*. This prairie species is recorded by Gray as escaped from cultivation only in Connecticut, while Britton & Brown say "escaped from cultivation in Connecticut, New Jersey, and Virginia." The present New York record seems worthy of note.

Thalictrum aquilegifolium L.—one plant found, at edge of woods, section 11, Pelham Bay Park, Bronx Co., N. Y., May 31, 1946, *H. Ahles 294*. This species is not listed in any current manual as having escaped anywhere in North America.

Trifolium pratense var. *albiflorum* Pluskal—in a meadow, Pelham Bay Park, Bronx Co., N. Y., July 23, 1946, *H. Ahles 662*. This albino form is not identified in any of the current popular manuals of American flora, but is listed in European works.

Vicia sepium L.—in thin woods, quite common, Pelham Bay Park, Bronx Co., N. Y., June 15, 1946, *H. Ahles 487*. Gray gives the American distribution of this European species as "locally, Me. to Ont."

Vicia villosa Roth—in meadow, section 5, Pelham Bay Park, Bronx Co., New York, July 11, 1946, *H. Ahles 475*. Gray says for this species "inclined to persist or escape," and Britton & Brown say "locally spontaneous." The present definite record seems worth noting.—HAROLD N. MOLDENKE.

PROCEEDINGS OF THE CLUB

Minutes of the Meeting of January 15, 1947. Dr. Simpson called the regular afternoon meeting of the Torrey Botanical Club to order at 3: 45 p.m. at the New York Botanical Garden. Seventeen members and friends were present.

No business was transacted and the meeting was turned over to Dr. Helen Purdy Beale who spoke on: "Some properties of Tobacco Mosaic Virus." Dr. Beale's talk was illustrated with lantern slides and was followed by much interesting discussion.

The meeting was adjourned at 5: 00 p.m. and was followed by refreshments served by members of the Garden's staff.

Respectfully submitted,
LIBERO AJELLO,
Recording Secretary

Minutes of the Meeting of February 5, 1947. The regular evening meeting of the Torrey Botanical Club, held in conjunction with the Brooklyn Botanic Garden's Plant Science Lectures, was opened by Dr. Shull at 8: 20 p.m. in the research building of the Brooklyn Botanic Garden. Thirty-one persons attended the meeting.

The minutes of the previous meeting were not read. Seven annual members and five associate members were presented to the Club for approval and all were elected unanimously.

No further business was transacted and the meeting was turned over to Dr. L. M. Black, who presented a very thorough and stimulating account of his research work on "Plant Tumors Induced by Viruses." A lively discussion followed the presentation of this fine paper.

The meeting was adjourned at 9: 45 p.m.

Respectfully submitted,
LIBERO AJELLO,
Recording Secretary

Minutes of the Meeting of February 19, 1947. The regular evening meeting of the Torrey Botanical Club was opened by Dr. Shull at 8: 00 p.m. at Columbia University with 24 members and friends present. The minutes of the meetings of January 15th and February 5th were approved as read.

The memorial to the late Dr. R. A. Harper, prepared by Dr. B. O. Dodge, Dr. H. W. Rickett and Dr. J. S. Karling was read before the members. Dr. Zimmerman moved that the Club send a vote of thanks and its compliments to the committee for their work. The motion was seconded and carried unanimously.

Dr. Shull read a letter from the Adirondack Club requesting the Torrey Botanical Club to cooperate in its efforts to prevent the granting of mining rights and the opening of recreational areas in the State's forest preserve. All members were urged to write to Senator Phiny W. Williamson protesting such a move.

No further business was transacted and the meeting was turned over to Dr. Ralph C. H. Siu, who spoke of his work at the Philadelphia Quartermaster Depot on the: "Fundamental Aspects of the Microbiological Degradation of Cotton." The paper was ably presented and provoked a lengthy discussion. The author's abstract follows:

> As a result of intensive work on the problem by the Quartermaster Corps, the N.D.R.C. and collaborating institutions, over 10,000 cultures of microorganisms have been isolated from deteriorated cotton fabrics. Of these, about 200 cultures have been shown to possess cellulolytic ability. It is doubtful, however, whether all these are of considerable importance under field conditions. In attacking the cotton fiber the fungal hypha penetrates the fiber wall into the lumen where it proliferates and digests the cotton fiber outwards. Bacteria, on the other hand, adhere to the outer surface and pit their way inwards. In both cases, the attack appears to be a highly localized affair with degradation occurring only at the point of the fiber in immediate contact with the microorganism.
>
> The organisms secrete cellulose-digesting enzymes. So far, these have been classified into 2 classes, viz.: (a) cellulase, which converts cellulose into cellobiose and (b) cellobiase, which converts cellobiose into glucose. Cell-free preparations of these cellulose-degrading enzymes have been made and their properties extensively studied.
>
> There are four general lines of approach to the development of preventive methods, viz.: (1) physical preventation of organism from making contact with the cellulose molecule, as illustrated by the resistance of resin-impregnated cloth, (2) cell toxicants, as exemplified by fungicides, (3) specific enzyme inhibitors which exist today as a theoretical possibility, and (4) chemical modification of the cellulose molecule, which appears to be very promising for future exploitation.

The meeting was adjourned at 9: 15 p.m. and was followed by tea prepared by members of the Columbia Botany Department.

Respectfully submitted,
LIBERO AJELLO,
Recording Secretary

Field Trip Reports

September 22. Butler to Pompton Plains, N. J. "Old Mother Nature sure did her part. The day was fine, the display of gentians was *much* the finest I ever saw in N. J., the orchids (*Spiranthes cernuua*) were there, literally in thousands, and the grapes were fully ripe and delicious." Leader, H. B. Gordon.

September 28. The New York Botanical Garden. "Because of the long stretch of dry weather, we found rather poor picking for the fleshy fungi. Special attention was given to a parasitic fungus, *Pseudonectria pachysandricola* on *Pachysandra*, which Dr. Dodge investigated and described. It was quite destructive to this host until Dr. Dodge worked out methods of controlling it." Attendance 16. Leaders, Fred J. Seaver and B. O. Dodge.

September 29. Dock Watch Hollow, N. J. An interesting host of woody and herbaceous plants was observed in this ramble through the Watchung Mountains hereabouts. No specialties were reported. Attendance 31. Leader, Harold N. Moldenke.

September 29. Princeton Jct. vicinity, N. J. This walk was a circular that included pond, stream, field, and woodland. The latter was observed in different aspects as we passed along Grover's Pond, crossed the Millstone River and returned along Plainsboro Pond. A comparative list of species would have been interesting for there are striking variations. Of course, with these leaders, many interesting bird experiences were adduced. Attendance 14, plus three who overshot the meeting place but caught up with the leaders in time to be counted. Leaders, Peg and Charles Rogers.

October 5. Southward from High Point, N. J. The Appalachian Trail survey and check for the Guide included the walk along the Kittatinny Ridge, descent to Lake Rutherford, and a visit to the shelters along this portion of the Trail. Some good views but no plant specialties reported. Attendance 9. Leader, L. E. Hand.

October 6. From Liberty Corner, N. J., westward on the Appalachian Trail. This list has not been compiled as yet. The Trail largely follows roadways here and some new species for the Trail List are expected. Attendance 11. Leader, G. G. Nearing.

October 6. Richmond, Staten Island. Although a bus strike prevented the leader's arrival, three people did make it and report a nice walk through old fields and over the salt marshes.

October 12. Woodlands, N. Y. "The ominous clouds distracted me to the point of overlooking a rich stand of *Solidago odora* I had meant to call attention to. We did notice a lot of *Solidago speciosa*, some *S. flexicaulis* and plenty of the more common goldenrods—*S. canadensis, S. rugosa, S. bicolor, S. caesia, S. graminifolia.* The various bushes provided a patriotic display of red, white, and blue berries, while the trees laid particular stress on the golden hues. The outstanding feature of the trip was an exceptionally profuse growth of *Baeomyces roseus* with exceptionally large pink fruiting bodies. An eight-year-old had the time of his life looking at the lichens through a lens. Said he, 'It is quite something to see so many things under the magnifying glass.' From his questions and remarks I am hopeful the little boy is a nature student in the making." Attendance 6. Leader, Alexandra Kalmykow.

October 13. Cheesequake Park, N. J. This walk over varied terrain featured the seeding and fruiting of plants as well as other aspects of dormancy in anticipation of the winter season. A great variety of edible fruits was sampled, most satisfying being the persimmons. A preliminary list of 400 seed plants and ferns so far determined from the Park is available from the field chairman upon request. Attendance 16. Leader, John A. Small.

OCTOBER 19. APPALACHIAN TRAIL BETWEEN CATFISH POND GAP AND MILLBROOK ROAD, N. J. This survey with its list of plants about completes the project from the Hudson River to the Delaware. There are a few places where one trip did not quite join where another left off. There are some five miles over Mt. Tammany and down to Columbia where the Trail has been relocated since our survey of the Dunnfield Creek route. Compilation is not completed yet. Has it been worth while? Shall we start along beyond the rivers? Attendance 12. Leader, Louis E. Hand.

NOVEMBER 10. LAKEWOOD, N. J. A very pleasant experience in the pine barrens in autumn. Lichen studies were added to the interesting notes on the higher plants. Attendance 17. Leader, James Murphy.

NEW NOTES

Alice Eastwood Herbarium Accessions. Miss Alice Eastwood, 88-year-old Curator of Botany of the California Academy of Sciences, reports that the Academy Herbarium, named in her honor, has received 9180 mounted specimens during the past year. Of these, 2978 accessions were by gift, 4722 by exchange with other herbariums, 1480 were by exploration. The Alice Eastwood Herbarium now contains a total of 334,000 mounted botanical specimens.

Wanted, Back numbers of the BULLETIN. The supply of back numbers of certain issues of the BULLETIN of the Torrey Botanical Club remaining in the possession of the Club are very low, and we are completely out of a few numbers. Unfortunately some of these numbers are of recent date and are in demand by foreign libraries which could not get the BULLETIN during the war, or which may have been destroyed. If any members have copies of the following numbers which they would be willing to donate to the Club we shall be very glad to receive them:

Vol. 67 (1940), Nos. 1, 2, 5, 6.
Vol. 68 (1941), Nos. 1, 2, 3, 4.
Vol. 70 (1943), Nos. 1, 2, 3.
Vol. 71 (1944), Nos. 1, 2.

They should be sent to Harold H. Clum, Business Manager, Hunter College, 695 Park Ave., New York 21, N. Y.

INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITOR OF THE TAXONOMIC INDEX

TAXONOMY, PHYLOGENY AND FLORISTICS

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